THE PROTEROSUCHIA AND THE EARLY EVOLUTION OF THE ARCHOSAURS; AN ESSAY ABOUT THE ORIGIN OF A MAJOR TAXON

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CONTENTS

ABSTRACT

After comments on several methodological and theoretical questions connected with the classification and the origin of major taxa, various hypotheses on archosaurian origins are discussed. A comparative survey of the characters of the early archosaurs, the proterosuchian thecodonts, shows that they are probably derived from the ophiacodont-varanopsid group of pelycosaurian synapsids. As the synapsids are known to have separated very early from the captorhinomorphs, and as the milleretids and younginids, which are captorhinomorph derivatives, are considered closely related to the origin of modern lepidosaurian orders, it is concluded that the two groups of diapsid reptiles, lepidosaurians and archosaurs, have quite different origins. A survey is also made of the present state of knowledge of the origin of the various archosaurian groups. The conclusion is that the final establishment of archosaurian orders as the dominant reptiles of the Jurassic and Cretaceous was the outcome of a gradual process, one which had an exploratory phase during the Middle and Upper Triassic. During this phase, various archosaurian lines of evolution developed, competing among themselves and with the therapsids in the exploitation of two basic food resources: green plants and animals. In the Upper Permian, the roles of plant-eaters and carnivores were mainly played by synapsids; from the uppermost Triassic to the end of the Cretaceous, they were mainly played by archosaurs. The origin

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of a major taxon is thus thought of as a long process involving several adaptive phases within the frame of the exploitation of food resources and of ecological competition. This process does not necessarily claim either the presence of special evolutionary processes or the acceleration of the rates of evolution in the transitional zone.

INTRODUCTION

The emergence and the rapid diversification of the archosaurian reptiles is one of the major events in the history of the vertebrates. During about 110 million years the terrestrial faunas of the world were dominated by the different dinosaur groups, which actually replaced, during Jurassic and Cretaceous times, most of the previously existing tetrapods in the exploitation of the varied terrestrial niches. During the same time another archosaurian group, the crocodiles, successfully occupied the freshwater, semi-aquatic, predaceous niche. Moreover, the Jurassic witnessed the first appearances of new major adaptive types among vertebrates: animals able to overcome the gravity barrier, the archosaurian order Pterosauria and the first birds, the latter being the most successful archosaurian derivatives surviving to the present time.

Disregarding the peculiar phenomenon of human evolution, we have to agree that the triumph of the dinosaurs and their relatives has been the major accomplishment in land vertebrate evolution, if we take as a criterion of evaluation the attainment of the greatest biomass by a single vertebrate group during the longest span of geological time. In this sense, the archosaurs have not been surpassed by any other vertebrate groups occupying the terrestrial environment. (The higher bony fishes in the seas have obviously surpassed the archosaurian achievement on land, but this does not matter in the present context.)

Many problems are posed by this empirical statement. The aim of science is to give causal explanations to observed phenomena, and we are far from being able to do this in the present case. However, we are at least able to draw the outlines of the framework within which such an explanation can eventually be attained. First of all, any metaphysical or pseudoscientific concept, such as "internal drive" or "phyletic senescence," must be excluded. Concepts of this kind are outside of scientific discourse, as they are untestable and do not sustain any kind of public demonstration of their existence. Instead, the phenomenon of archosaurian expansion and dominance may be thought of as part of a vaster and more complex phenomenon of life expansion within an entire ecosystem, since the rise of a land vertebrate biomass requires an even greater expansion of the biomass within the first trophic level, that of the green plants. However, one of the more important requirements for understanding such a phenomenon is a thorough and accurate knowledge, at the descriptive level, of the events leading to the dominance of archosaurs during the different phases of their evolution. In this sense, the first steps of archosaurian evolution and, indeed, the very emergence of the group are of paramount importance.

The first steps in archosaurian evolution took place during Triassic time, and the group attained dominance during the early Jurassic. The fossil record shows that the Triassic witnessed a major overturn in the distribution of roles in the food-web relationships: the roles of herbivores and carnivores during Permian and early Triassic times were mainly filled by synapsids, whereas during Jurassic and Cretaceous times, these roles were filled by archosaurs.

The Triassic, then, was the period during which the archosaurs became dominant. Once having achieved their dominance, they held it during two entire geological periods. However, the rise of the archosaurian orders was actually accomplished at the very end of the Triassic, and was a step-wise process, in which several lines evolved and became extinct. The principal archosaurian roles were played during these first steps by taxa currently included in the order Thecodontia. One can say that the archosaurians had a first, exploratory radiation before their main one, a radiation that took place within this order of the thecodonts.

The very beginning of this exploratory radiation was developed during early Triassic times by a very primitive and atypical archosaur group, the Proterosuchia, usually grouped as a suborder of the Thecodontia. The proterosuchians are hence the stem archosaurs, the stock from which most of the later archosaur groups took their origin. An adequate understanding of them is thus essential for a good interpretation of all the further events of archosaurian evolution.

Knowledge of the Proterosuchia has been very unsatisfactory until recently. Fortunately, during the last ten years (and especially during the very last part of this period), descriptions of new materials and thought-provoking revisions have shed new light, thus helping us to reach a better understanding of the group. As usual in scientific progress, new knowledge leads to new problems, and our progress in the understanding of these primitive thecodonts poses several new questions. The general outlines of archosaurian evolution are now in need of a thorough revision, and the whole problem of the origin of this subclass must be approached in a new way because of the improvement of our knowledge of the Proterosuchia. Nevertheless, neither of these goals can be adequately achieved before a good assessment of the bearing of proterosuchian peculiarities on archosaurian evolution is available. The assessment of these peculiarities also poses a problem in classification. The aim of this paper is to stress the general evolutionary significance of the characters of this group of primitive thecodonts and to stress some methodological points that arise in our attempt to place them in an evolutionary classification.

As the stem group of a major taxon, the Proterosuchia set forth some interesting classification problems for the theory of evolutionary systematics, which will also be discussed in the following pages.

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FOUNDATIONS

Some theoretical points are worth stating before discussing our topic. Authors frequently disagree for the simple reason that the one is not aware of the underlying concepts of the other. This is especially true when the concepts are controversial in nature. As most of our argument deals with supraspecific taxa, it will be convenient to assess the sense we give to this concept.

A supraspecific taxon is not here thought of as a mere artifact created to fulfill the aims of taxonomic practice. It is considered a natural group, a historico-spatial entity formed by various subordinate taxa connected among themselves by special evolutionary relationships: common origin, links of descent, and a common evolutionary role. The origin of a supraspecific taxon is not here assumed to be the outcome of special evolutionary processes. We take for granted that the known short-term processes of evolution at the species level are also the causal agents responsible for the establishment of major taxa over long-term evolutionary processes. But as the scale of the latter processes allows and requires more general descriptive concepts, we can also say that, in the emergence of supraspecific taxa, anagenesis, cladogenesis, and extinction are involved. The type of anagenesis here operating is the "open anagenesis" (Waddington, 1960) or arogenesis (Reig, 1963b). Arogenesis is associated with the acquisition of a new "basic general adaptive complex" (Simpson, 1959: 270). Other authors name these kinds of acquisitions "Erfindungen" (Rensch, 1947) or "key innovations" (Bock, 1965). It is commonly supposed that the emergence of these novelties is responsible for opening the possibility of exploiting new adaptive areas to the new taxon, thus promoting its splitting to fill up new ecological niches and situations (cladogenesis). We want to emphasize that the extinction of the groups previously exploiting the same ecological niches may be a triggering factor for the emergence of the new taxon. This extinction may also be thought of, however, as provoked by the rapidly evolving, and better adapted, emerging new taxon.

Another attribute of a supraspecific taxon is monophyly. As this concept is rather controversial, we will enunciate the two extreme possibilities for the fulfillment of this condition: a monophyletic group may be considered as either a group originating from a single ancestral species or, at the least, a group originating in a taxon of the same rank.

Supraspecific taxa originate by the differentiation from an original group of a new group showing new characteristics (Sharov, 1965). It has been generally assumed that in this process of the differentiation of a new group the shift of the evolving organisms into a new adaptive zone is a necessary condition. Such a shift would then involve a threshold effect, and the rate of evolution would be accelerated in the transitional area. Simpson (1953) named this supposed phenomenon "quantum evolution," pointing out that the period of rapid transition involved in such a process may serve to establish comparatively nonarbitrary divisions among major taxa (Simpson, 1961). Gisin (1966), in developing the same ideas, emphasizes that the "evolutionary quantum" affords the main criterion for the definition of taxonomic groups. As far as the theory of classification is concerned, he defines the concept of evolutionary quantum as follows: "Un quantum n'est pas la somme de toutes les différences, mais celle des caractères clefs développés lors de l'évolution quantique du groupe, autrement dit, les caractères sont pesés en fonction de leur signification évolutive" (Gisin, 1966: 4). Gisin refers to these ideas as a "quantum theory of taxonomy," a development of his former "synthetische Theorie der Systematik" (Gisin, 1964). It seems obvious to the present author that all these concepts are better considered as part of the approach already named "evolutionary taxonomy" (see Mayr, 1965).

We believe that these principles give a sound basis for the assumption that natural groups have (or had, in the case of extinct groups) a real existence in nature as objective, historico-spatial collective entities, their unitary character being given by evolutionary relationships linking their different subordinate constituents. Nevertheless, these natural groups (having existence in the ontic level; see Bunge, 1959) are not to be confused with the taxon-concepts we construct about them (existing in the cognitive or conceptual level). Systematists hypothesize that a given set of species belongs to a supraspecific taxon, that a constructed taxon-concept matches a natural taxon. When we say that a given number of species of Lower Triassic thecodonts are to be placed together in the suborder Proterosuchia, we are dealing with a taxon-concept (the suborder Proterosuchia) that we construct for a taxon we believe to have existed in nature. In this sense, the construction of a taxon-concept is equivalent to the statement of a hypothesis (Reig, 1968).

It must be stressed that, as with any scientific hypothesis, these evolutionary-taxonomic hypotheses may never be claimed to have reached a status of certainty after having been "proved." These hypotheses may be stronger or weaker, more or less well founded, but they can never be transformed into a fully certain piece of knowledge, certainty not being at the core of the scientific way of thinking. Nevertheless, this assessment does not obviate the necessity of trying to make our hypotheses match as closely as possible the events for which they are erected. The likelihood that an hypothesis closely approximates natural events will be greater if it is able to support testing procedures, if it has a high explanatory value, and if its predictions are infalsifiable (see Popper, 1959; Wilson, 1965). If the hypothesis fails to fulfill these requirements, clearly it must be rejected as a tool for understanding natural events.

By the very nature of paleontological evidence and of taxonomic-phylogenetic inference, we must admit from the start that fully satisfactory testing procedures for this kind of hypothesis have not yet been developed (for an interesting and thought-provoking discussion of this topic see Goudge, 1961). In most cases, in order to accept it, we must take refuge in its heuristic value or in such attributes as its internal coherence or accordance with available scientific knowledge. This means that the foundations of our argument could be very weak if we are not careful to clarify our taxonomic concepts as far as the available evidence and theory permit.

As with any concept, the taxon-concepts have intension (connotation) and extension (denotation). The intension of a taxon-concept is the set of peculiarities that determine its own nature, that is, the set of characters that distinguishes it from others. Its extension is the set of subordinate taxa that belong to it.

The taxon-concepts are polythetic concepts, as defined by Beckner (1959; Beckner named these kinds of concepts "polytypic concepts," and the name "polythetic" was introduced later by Sneath, 1962). For a better understanding of the nature of polythetic concepts, see also Sokal and Sneath (1963). Membership in a polythetic group is not decided by the complete sharing of a set of sufficient and necessary features. Sufficient and necessary properties are useful for classifying static entities, but not evolving organisms. In other words, any taxon-concept, for the very reason that it is intended to approximate an evolving entity, must be defined by reference to a set of characters that are assumed to be evolving in the frame of the taxon itself. Thus no claim is to be made that any member of the taxon must present all the relevant characters in the defined state, nor that any form must necessarily belong to it because it possesses one or a few of the stated characters.

Acceptance of these points makes it possible to understand why the Proterosuchia are to be considered archosaurs in spite of the fact that they lack many of the relevant archosaurian peculiarities, such as the full development of an otic notch or the habitually upright stance, and why the euparkeriids need not necessarily be considered proterosuchians, although they share with them some primitive characters.

Yet a taxon-concept cannot be a full polythetic class in the sense of the third condition pointed out by Beckner, a condition asserting that membership in a particular aggregate does not of necessity require the possession of a given character. Actually, the intension of a taxon-concept must include one character or a limited number of characters, the possession of which is necessary for membership in the said concept. Otherwise, our theoretical assumption that a taxon evolves through the acquisition of defined "key innovations" is not fulfilled.

These foundations may be considered the theoretical and formal tools for approaching our topic within the framework of evolutionary systematics. We think the approach of evolutionary systematics has greater depth, is far more explanatory in nature, and accords better with modern evolutionary thought than do others, such as the cladistic approach (e.g., Hennig's "phylogenetisches Systematik") or the neo-Adansonian phenetic one.

THE EXTENSION OF THE PROTEROSUCHIA-CONCEPT

The first point to make clear in our attempt to elucidate the taxon-concept involved in the name "Proterosuchia" is the assessment of its extension. Though some sort of circular reasoning is unavoidable, it seems evident that the inferential process that leads to the construction of a taxon-concept begins with the failure to assign certain taxa to existing taxa of higher rank, thus revealing the existence of a previously unknown taxon. The concept of this taxon is now constructed on the basis of a need for a group to contain certain definite subordinate constituents. Needless to say, it is the peculiarities of the subordinate members that fail to find a place in existing taxa that indicate that these members need to be referred to a new taxon. However the intension of the latter can only be fully assessed after it is clear which are its members.

Charig and Reig (in press) have made an extensive survey of the genera to be included within the Proterosuchia and have discussed Hughes's broad conception and interpretation of this taxon (1963). It is unnecessary to repeat here the arguments developed in that paper, but a summary of the conclusions and further discussion of some points are relevant to the present topic: that Proterosuchia include only, so far as is presently known, one Upper Permian and several Lower Triassic genera. Most Lower Triassic archosaurs are proterosuchians, the only exceptions being *Mesorhinosuchus*, *Euparkeria* (including *Browniella*), and the doubtful *Wangisuchus* and *Fenhosuchus*. Some Middle and Upper Triassic archosaurs occasionally referred to the Proterosuchia, such as *Rauisuchus*, *Dasygnathoides*, *Hoplitosuchus*, *Saurosuchus* and *Stagonosuchus*, are well enough known to be excluded from this group (Reig, 1961; Charig and Reig, in press).

All the known proterosuchian genera seem clearly to fall into two distinct subordinate taxa of family rank, for which it is advisable to use the names Proterosuchidae and Erythrosuchidae. The former is the older, more primitive, and more aquatic group. The latter family is almost surely derived from the proterosuchids, appears later in the fossil record, is more advanced, and seems to have been composed of largely terrestrial carnivores.

The Proterosuchidae include the following genera: *Archosaurus* (1 species, from the Upper Permian Russian Zone IV); *Chasmatosuchus* (2 or 3 species, from the Russian Zone V, lowermost Triassic); *Chasmatosaurus* (Figs. 1, 3, 5) (3 or 4 species: one in the *Lystrosaurus* Zone, lowermost Triassic, South Africa, another in beds of the same age in Sinkiang, China, another in the Chinese Ermaying Series, late early Triassic, and a probable fourth unnamed species in the Panchet Series of Bengal); *Proterosuchus* (1 species, probably from the *Procolophon* Zone, middle

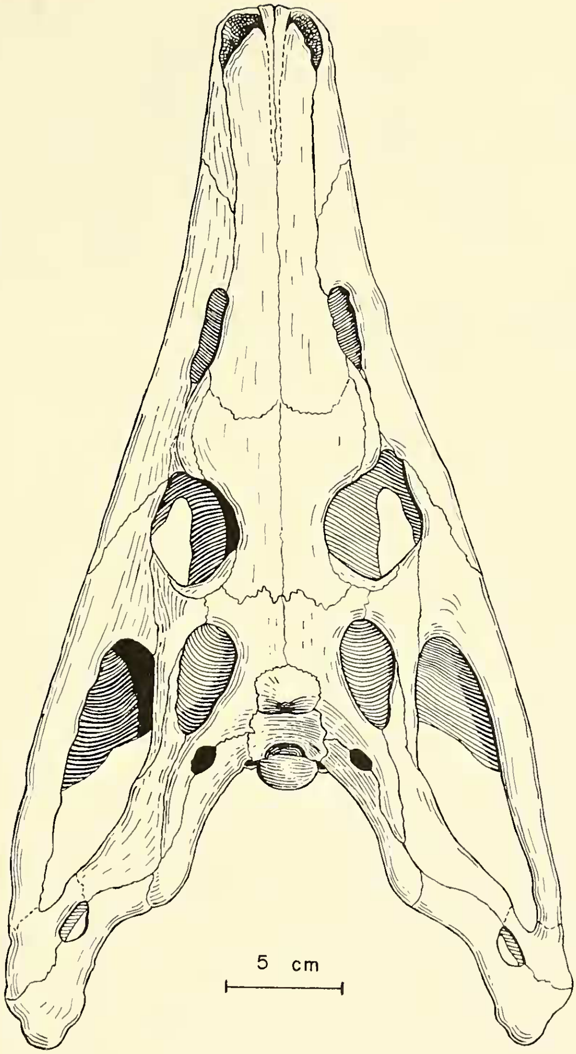

Figure 1. Dorsal view of the skull of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

Lower Triassic of South Africa); and *Elaphrosuchus* (1 species, from the *Lystrosaurus* Zone, South Africa).

The Erythrosuchidae includes the following genera: *Garjainia* (Fig. 2) (1 species, from the Russian Zone V, lowermost Triassic); *Erythrosuchus* (1 species, from the *Cynognathus* Zone, late early Triassic, South Africa); *Vjushkovia* (Fig. 4) (1 species, from the Russian Zone VI, late early Triassic); and *Shansisuchus* (1 or 2 species, from the Chinese Ermaying Series, late early Triassic).

Cuyosuchus (1 species, Cacheuta beds, Lower Triassic, Argentina) must be considered as Proterosuchia *incertae sedis,* as the material is not sufficient for family allocation. *Ankistrodon, Arizonasaurus, Dongusia, Seemania,* and *Ocoyuntaia* are generic names applied to material that may prove to be referable to the Proterosuchia, but which must be considered

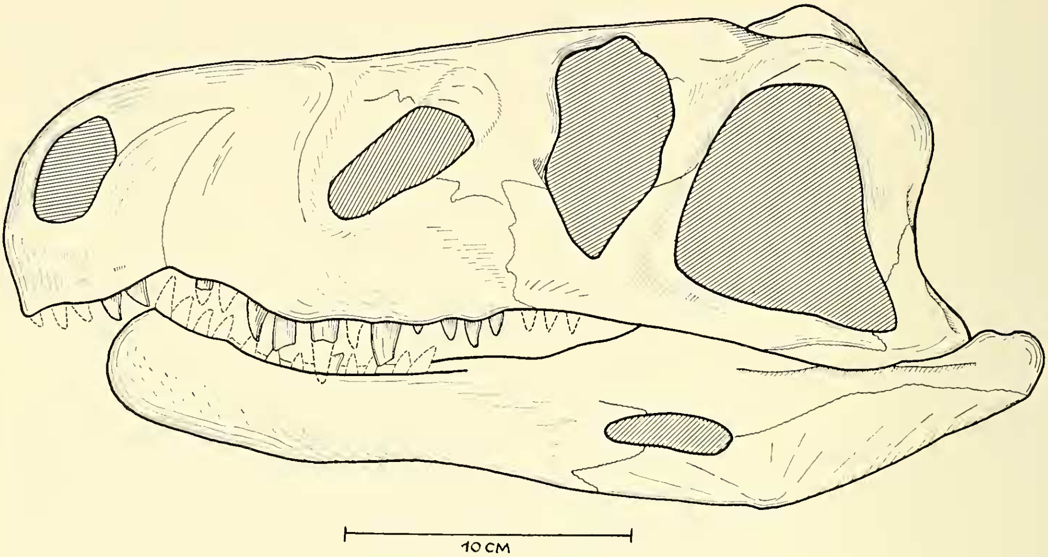

Figure 2. Lateral view of the skull of *Garjainia prima* Ochev. (From Ochev.)

nomina dubia for the present because the specimens are extremely fragmentary.

As these last remarks imply, not all the above-mentioned genera are really well known, and some are based on material too incomplete for adequate knowledge of all relevant characters. All evidence considered, however, we have a fairly good knowledge of at least the genera *Chasmatosaurus, Erythrosuchus, Vjushkovia, Shansisuchus,* and *Cuyosuchus,* from all of which a good part of the postcranial skeleton is known. The other genera that permit family allocation are known from less complete material. They are very useful, however, either to infer phylogenetic conclusions, as in the case of *Elaphrosuchus* and *Garjainia,* or to improve knowledge of the temporal and geographical distribution of the groups concerned.

Nevertheless, we must admit that we know only a very small part of the actual proterosuchian array, and this must be carefully kept in mind when discussing early archosaur evolution. It must be taken for granted that many proterosuchians existed that are at present unknown, and that among them might lie the direct ancestors of later archosaurs, which are not easily to be detected among the forms we know at present. This kind of assumption is the very basis of paleontological inference.

THE INTENSION OF THE PROTEROSUCHIA-CONCEPT

The Proterosuchia are such a puzzling group that von Huene was inclined, in one of his first works (1911), to place one of the included genera, *Erythrosuchus,* in an order of its own, sharing pseudosuchian and pelycosaurian features. As stressed by Hughes (1963), they combine some truly archosaurian peculiarities in the skull and other parts, with primitive, non-archosaurian characteristics in the limbs and girdles. As we shall see below, some non-archosaurian features are also present in the skull structures.

Hughes made a careful analysis of the peculiarities of the Proterosuchia, but he emphasized primarily postcranial morphology. Romer (1956, 1967), on the other hand, pointed out the significance of very

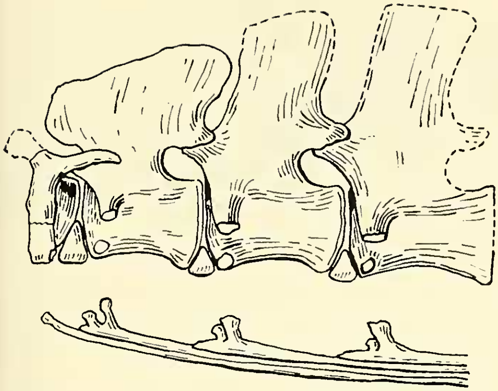

Figure 3. Cervical vertebrae and ribs of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

peculiar proterosuchian skull characters, neglected by Hughes and other authors. Charig and Reig (in press) list the state of many characters in this taxon, but they do not discuss thoroughly their evolutionary significance. A further analysis, therefore, seems necessary.

Statement and analysis of the proterosuchian character-states

Following Sokal and Sneath (1963), we shall use the character-state terminology in our present analysis. For these authors, a character is a variable that can occur in different states from one kind of organism to another. These character-states are the relevant features that taxonomists deal with in comparing different taxa. For instance, "dermal ossifications" is a character, and "dermal ossifications absent" is a character-state.

Since they belong to a taxon of higher rank, the subclass Archosauria, the Proterosuchia have a set of character-states shared by all archosaurs. We shall refer to this set of character-states as the "All-Archosaurian set of character-states" (*AA*). This *AA* set represents the intension of the taxon-concept Archosauria, and should not afford a relevant basis for elucidating the concept of Proterosuchia, though its assessment is very important to support the

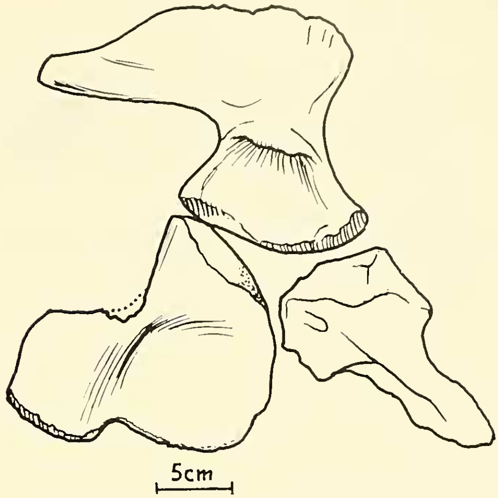

Figure 4. Lateral view of the pelvis of *Vjushkovia triplicostata* von Huene. (From von Huene.)

inclusion of the Proterosuchia in the Archosauria and for an enquiry regarding the origin of the whole subclass. The following list includes the character-states that we consider as belonging to this set:

i) Two-arched skull (diapsid condition)
ii) Antorbital fenestra present
iii) Mandibular fenestra present
iv) Laterosphenoid ossified
v) Skull metakinetic
vi) Quadrate-squamosal articulation moveable
vii) Supratemporal and tabular bones absent
viii) Posttemporal fenestrae small
ix) Vertebrae not notochordal
x) Ribs with capitulum and tuberculum
xi) Rib facets of dorsal vertebrae on transverse processes, becoming closer to a complete fusion posterad
xii) Capitular facets for cervical ribs situated well anteriorly and ventrally on the centrum; tubercular facets for the same ribs at the tip of transverse process
xiii) Posterior limbs longer than anterior (limb disparity)

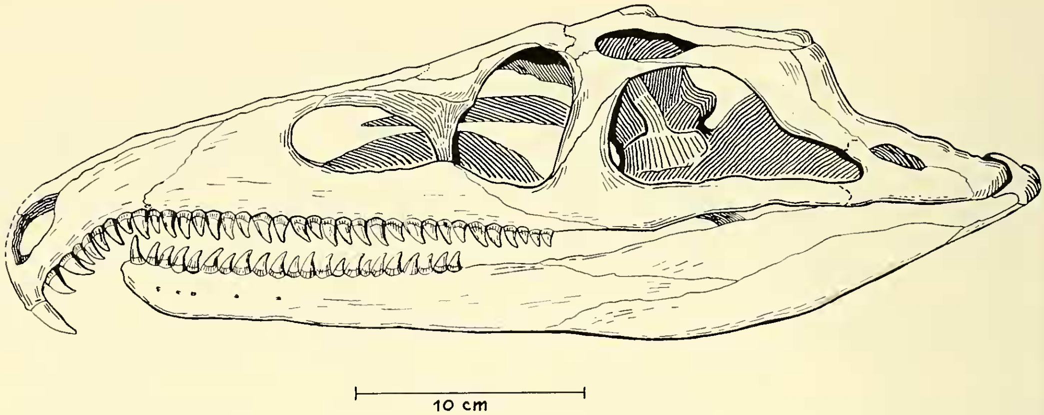

Figure 5. Lateral view of the skull of *Chasmatosaurus vanhaepeni* Haughton. (From Broili and Schröder.)

Some allegedly characteristic archosaurian character-states, such as upright stance and bipedalism, are not included in this list. As has been suggested by Charig (1965), they are neither characteristic nor widespread archosaurian features.

The core of our discussion should be connected with those character-states that would help to define the Proterosuchia as distinct from other taxa included in the Archosauria. These character-states may be grouped in four different classes: (a) the All-proterosuchian-No-other-archosaurian set of character states (*AN*), which includes peculiarities shared only by the proterosuchians, absent in any other archosaurian taxon; (b) the Some-proterosuchian-No-other-archosaurian set (*SN*), comprising characters that are present in the described state only in some of the proterosuchians, while present in a different state in other proterosuchians and in all the other archosaurs; (c) the All-proterosuchian-and-Some-other-archosaurian set (*AS*), including character-states shared by all the members of the extension of the Proterosuchia, but also present in some other non-proterosuchian archosaurs; (d) the Some-proterosuchian-and-Some-other-archosaurian set (*SS*), referring to those character-states shared by some, but not all the members of the Proterosuchia, and also by some, but not all, archosaurian groups not belonging to the Proterosuchia.

The following list attempts to synthesize the relevant character-states of the Proterosuchia. The letters preceding each statement refer to the above-defined sets.

1. (*AS*) A single median postparietal bone present
2. (*AS*) Small postfrontal bones present
3. (*SN*) A small pineal foramen present
4. (*AN*) A typical otic notch not present
5. (*AN*) The posterior border of the infratemporal fenestra nearly straight (without the V-shaped contour characteristic of most archosaurs)
6. (*AS*) The jaw articulation well behind the level of the occiput
7. (*AS*) Antorbital fenestra of moderate size, not opening as a part of a more extended, basin-like depression
8. (*AS*) Nares of moderate size, subterminal, fairly well separated from the antorbital fenestra
9. (*AS*) Pterygoids not meeting in the midline, bordering a long and narrow interpterygoid vacuity extending forward between the vomers

10. (*SS*) Palate with teeth in the pterygoid flanges
11. (*AN*) Occipital plane rather concave, slanting forward towards the skull table
12. (*AS*) Prefrontal bones large, projecting laterally to form a ridge that makes an abrupt limit between the roof of the skull and the lateral antorbital region
13. (*AN*) Marginal teeth isodont and acrodont or subthecodont in implantation
14. (*SS*) Intercentra usually present behind the axis, more commonly between the cervical vertebrae
15. (*AS*) Gait quadrupedal
16. (*AN*) Propodials horizontal in position (sprawled stance)
17. (*AN*) Posterior limbs moderately longer than the front ones (primitive limb disparity)
18. (*AN*) Femur bearing a large internal trochanter
19. (*AN*) Intertrochanteric fossa of the femur present
20. (*SS*) Humerus with wide and twisted ends
21. (*AN*) Pes with mesotarsal ankle joint (proximal tarsals without specializations)
22. (*AS*) Iliac blade with anterior spine absent or only moderately developed
23. (*AS*) Posterior expansion of the iliac blade narrow and long
24. (*AS*) Acetabula completely closed, only moderately excavated, and relatively far apart one from the other
25. (*AS*) Pubis and ischium comparatively short
26. (*AS*) Coracoids large
27. (*SN*) Scapulae broad and short
28. (*AS*) Dermal elements of the pectoral girdle well developed
29. (*AS*) Dermal armor of any sort absent

From the above list of character-states, interesting conclusions can be drawn, but it is first necessary to make a brief analysis of them.

(1) The possession of postparietal bones (Fig. 1) (interparietal, dermosupraoccipital) is a primitive condition for reptiles, and is widespread in such primitive groups as the cotylosaurs, the pelycosaurs, the eosuchians, and the millerettids. This character-state is shared by all the genera assigned to the proterosuchia, in the form of an unpaired postparietal. However, this is not an exclusive proterosuchian condition among the archosaurs, as a postparietal is also present in the pseudosuchian thecodont *Euparkeria*.

(2) Postfrontal bones (Fig. 1) are also present in most primitive reptile groups and in all the proterosuchians so far known. As in the former case, other non-proterosuchian archosaurs retain this primitive state, as postfrontals are present not only in *Euparkeria* but also in the phytosaurs, the stagonolepidid pseudosuchians, and the rhamphorhynchoid pterosaurs.

(3) A pineal foramen is, as far as is known, present only in all the known specimens of the erythrosuchid genus *Erythrosuchus*, in the primitive erythrosuchid *Garjainia* (see Tatarinov, 1961: 121), and in one of three known skulls of *Chasmatosaurus*. Other proterosuchian genera either have been reported as not possessing this character, or cannot be checked due to the nature of the material. Among other non-proterosuchian archosaurs, this character is absent, save in one doubtful genus, *Mesorhinosuchus* (=*Mesorhinus auct.*), currently considered the only Lower Triassic phytosaur. We are also dealing here with a very primitive state of a character, present as such in the earliest reptilian groups.

(4) Romer pointed out (1956, 1967) the absence of a typical otic notch in the Proterosuchia. He based his statement on the genera *Chasmatosaurus* (Fig. 5) and *Erythrosuchus. Garjainia* (Fig. 2), *Shansisuchus,* and *Vjushkovia* give support to the same view. The latter genus has indeed been reconstructed by von Huene (1960) as having a well-developed otic notch, but this reconstruction is purely hypothetical and is not supported by the morphology of the surrounding parts. Tatarinov (1961) has indicated that the posterior border of the infratemporal opening was straight in *Vjushkovia,* as in *Erythrosuchus,* a feature correlated, in other proterosuchian genera, with the absence of a defined otic notch. In all proterosuchian skulls, therefore, the construction of the otic region is very primitive. This recalls the pelycosaurian and captorhinomorph condition and differs from all remaining archosaurs and from lepidosaurs (including millerettids and eosuchians, in which a distinct lepidosaurian otic notch is clearly present). In all non-proterosuchian archosaurs the otic notch is clearly defined by a curved posterior border of the quadrate and by a projection of the squamosal, which extends posteriorly above the head of the quadrate to form the dorsum of the notch. The character-state "absence of the otic notch" hence belongs obviously to the *AN* set.

(5) Linked with the otic notch is the shape of the posterior border of the infratemporal fenestra. The V-shaped contour of this border, with the apex of the V facing forward, is common to all the non-proterosuchian archosaurian genera (save those with secondary modifications from a primitive V-shaped condition). In connection with the posterior position of the mandibular articulation, the quadrate of the proterosuchians slants sharply backwards. The ascending ramus of the quadratojugal and the descending ramus of the squamosal follow the quadrate in this position. In more advanced archosaurs, the jaw articulation moved forward, apparently in connection with the development of a more efficient biting mechanism (Ewer, 1965), and the quadrate acquired a more vertical position. In this position of the quadrate, the V-shape of the quadratojugal and squamosal arms is obligatory, and, consequently, room is developed for an otic notch, further enlarged by the backward projection of the squamosal. The proterosuchian condition of this character is again a primitive one, as this is the state shown by the pelycosaurs, especially by the varanopsid pelycosaurs. The assumption that this condition is shared by all the proterosuchians is safe, and the same is valid for character-state 4, as it is present both in primitive (*Chasmatosaurus*) and advanced genera in which the skull is known (*Erythrosuchus, Shansisuchus*). Therefore, this is to be considered an *AN* character-state.

(6) As far as the position of the jaw articulation is concerned, this character obviously belongs to the same cluster as the two previously described. All the proterosuchian skulls so far known show a backward position of the suspensorium (Figs. 1, 2, 5), the articular condyles for the mandible lying in a line well posterior to the line of the occipital condyle. This condition is distinctly different in the non-proterosuchian archosaurs, save the primitive crocodile *Proterochampsa* and, in a lesser degree, some phytosaurs. Character-state 6 belongs therefore to the *AS* class. Romer (1967) pointed out that this long-jawed condition is characteristic of very primitive reptiles and is reminiscent of the captorhinomorph skull architecture. In primitive pelycosaurs of the ophiacodont-varanopsid group this character-state is even more pronounced, but both the millerettids and the eosuchians are more progressive in this respect.

(7) The presence of an antorbital fenestra is a characteristic archosaur character-state. It is safe to consider the

condition of the character in the proterosuchians as primitive, as in them the fenestra does not reach a large size and, especially, as it does not lie in a depression with sharp borders, as is the case in most other thecodonts and other archosaurs. Though the function of this fenestra is not completely clear (Ewer, 1965; Walker, 1961), it is obvious that whatever its function may have been, its increase in size, and the development of a basin-like structure to contain it are to be considered as an intensification of the function; the structure was not fully developed in the proterosuchian level of archosaurian evolution. The described proterosuchian state of this character seems to be shared by all the known skulls (Figs. 2, 5) referred to this taxon, with *Shansisuchus* as an atypical example, since this genus has the peculiarity (also present in some saurischian dinosaurs) of having an additional opening, though not a basin-like depression. *Vjushkovia* has been restored by von Huene with a great antorbital opening, but again this seems clearly to be a quite tentative reconstruction, as most of the borders of the fenestra are not preserved in the known specimens. The fact is that other, non-proterosuchian, archosaurs share this state of the character, as is shown in the primitive crocodile *Proterochampsa,* in the peculiar pseudosuchian *Rhadinosuchus* (=*Cerritosaurus*), in *Clarenceia*, and in the phytosaurs. This character-state is therefore to be considered as belonging to the *AS* class. It is indeed very suggestive that an antorbital fenestra, elsewhere only an archosaurian character-state, is present in the varanopsid pelycosaurs (Olson, 1965, and see also below).

(8) The described state of the external nares is shared by all the proterosuchian genera (Figs. 1, 2, 5). More advanced thecodonts usually have the external nares larger and nearer to the antorbital vacuity, or else posterior in position (phytosaurs). Subterminal, small nares well separated from the antorbital opening are also present in *Rhadinosuchus* and *Clarenceia*, and the situation in *Euparkeria* is best considered reminiscent of the proterosuchian state. This character-state must therefore be grouped in the *AS* category.

(9) This character-state is inferred from the condition in *Chasmatosaurus*, the only proterosuchian in which the palate is well known. Inasmuch as the same condition is shared in such a probable erythrosuchid-derivative as *Euparkeria,* it is safe to conclude that this state was widespread among the proterosuchians. Among other archosaurs, it is shared not only by *Euparkeria,* but also by *Proterochampsa,* so that the character-state must tentatively be considered as belonging to the *AS* class.

(10) The presence of palatal teeth in the pterygoid flanges has been verified in *Chasmatosaurus* and *Proterosuchus* among the proterosuchids, but no erythrosuchid has given any evidence of them. Palatal teeth are known among archosaurs, other than proterosuchians only in *Euparkeria* and in *Proterochampsa* (Sill, 1967). This state of the character is obviously a primitive one, as palatal teeth are present in millerettids, younginids, procolophonids, pelycosaurs, and captorhinomorphs among the primitive groups. It must hence be placed, so far as present knowledge allows, in the SS class.

(11) This is a peculiar, primitive, and pelycosaur-like state of the occipital region. All the proterosuchian genera in which the character can be checked show this state clearly; it is especially evident in *Chasmatosaurus.* No other archosaur shows a similar condition, so that this feature is to be allocated to the *AN* class.

(12) This state of the prefrontal is not a proterosuchian peculiarity, as it is also characteristic of many thecodonts that are not proterosuchians and of some saurischians. The condition is also shared by some non-archosaurian reptiles, such as the

ophiacodont and varanopsid pelycosaurs. This fact suggests that we are confronting a primitive character-state that evolved slowly within the archosaurs. As it is shared by all the proterosuchians so far known, it must be placed in the *AS* class.

(13) In all proterosuchians so far known, the marginal teeth are isodont and either acrodont (proterosuchids) or subthecodont (erythrosuchids); true heterodonty and thecodonty are not clearly developed in either group. All non-proterosuchian archosaurs are definitely thecodont in tooth implantation, and their teeth are primitively heterodont or subheterodont. The proterosuchian condition is also a primitive one, widespread among the earliest reptiles and their first derivatives. This character-state must hence be placed in the *AN* class.

(14) Another primitive condition reminiscent of the seymouriamorph, captorhinomorph, pelycosaurian, and early lepidosaurian condition, is the presence of intercentra. This has been clearly demonstrated in the neck vertebrae of *Chasmatosaurus vanhoepi* (Fig. 3), and Young (1963) has described the same situation in the trunk vertebrae of *Chasmatosaurus yuani.* Neck intercentra have been reported in *Erythrosuchus*, but seem not to be present in *Shansisuchus, Garjainia, Vjushkovia,* and *Cuyosuchus.* In later archosaurs, intercentra have not been reported in any genus save *Euparkeria*, where they seem to be present all along the presacral region of the column. Another (abnormal) exception is the rauisuchid *Ticinosuchus*, which is alleged to have had an intercentrum associated with one of the caudal vertebrae (Krebs, 1965). We are dealing therefore with a feature of the SS class.

(15) The quadrupedal gait is, of course, a character-state shared by all the known proterosuchians, but obviously common, too, in many non-proterosuchian archosaurs, such as the euparkeriids, the rauisuchids and the stagonolepidids among the thecodonts, the crocodiles and phytosaurs, and many groups of saurischians and ornithischians. This is obviously a primitive reptilian feature, and must hence be placed in the *AS* class.

(16) The position of the propodials has been inferred by Hughes (1963) to be horizontal in the known proterosuchians. Nevertheless, Young's (1964) reconstruction of the skeleton of *Shansisuchus* shows the propodials in a vertical position, which is probably also reasonable. Completely sprawled legs would not have allowed large terrestrial animals such as the erythrosuchids to be successful predators, and the evidence seems to indicate that they had a time of success during the Lower Triassic. It is probable that all the proterosuchians had a sprawled stance most of the time, as indicated by the anatomical data, but that at least the advanced erythrosuchids could proceed in a largely upright stance for short distances. In any case, it is obvious that the proterosuchians sprawled more than any later archosaur, and that this state was shared by all the genera that afford relevant evidence in the girdle and limb skeletons. As stated by Ewer (1965), *Euparkeria* also seems to have had a sprawled stance, but this genus seems to have been far more advanced than the proterosuchians as far as locomotion is concerned. This feature can therefore safely be considered to be in the class of the *AN* character-state.

(17) This character-state is a typical archosaur one, though it has been exaggeratedly associated with bipedalism, which is not only not a widespread condition in archosaurs, but is not even a primitive archosaurian characteristic (Charig, 1965). Charig has named this condition limb-disparity, and though characteristically archosaurian, it must be noticed that this is also present in the ophiacodontid and varanopsid pelycosaurs. Limb disparity may be considered a preadaptation for

bipedalism, but is less marked in the Proterosuchia than in more advanced archosaurs. In the known cases, for instance, the humerus/femur ratio is never lower than 77.7 in the proterosuchians, and is always lower than 67 in the non-proterosuchian thecodonts. This might be therefore considered an *AN* character-state.

(18), (19) The possession of an internal trochanter and of an intertrochanteric fossa is alleged by Hughes (1963) to be a full indication of the sprawled position of the legs. As far as is known, all proterosuchian femora share in the possession of these characters. The pelycosaurs and captorhinomorphs share the same character-state, but none of the known non-proterosuchian archosaurs have either an internal trochanter or an intertrochanteric fossa. Hughes assumed that the Argentinian rauisuchid *Saurosuchus* shared the proterosuchian state of these characters, but this is a misinterpretation of the illustrations given by Reig (1961), as Charig and Reig (in press) have already made clear. These character-states hence belong to the *AN* class.

(20) The structure of the humerus is well known in *Chasmatosaurus* (Young, 1963), *Erythrosuchus, Shansisuchus, Vjushkovia,* and *Cuyosuchus* (Rusconi, 1961, wrongly described this bone in *Cuyosuchus* as the femur of the labyrinthodont *Chigutisaurus*). In all these genera the ends are twisted, but in the last they are not typically wide, as is the case in the other four genera. Humeri with wide and twisted ends are also present in the rauisuchid *Stagonosuchus* (von Huene, 1938; Boonstra, 1953) and in the problematic Argentinian Middle Triassic genus *Argentinosuchus* (Casamiquela, 1961). This may be considered a primitive character-state, as it is also present in the pelycosaurs and captorhinomorphs. In any case, the exception of *Cuyosuchus* and the presence of the same state in other non-proterosuchian thecodonts, indicate that it is convenient to place this feature in the SS class.

(21) The structure of the feet in the proterosuchians has been elucidated by Hughes (1963) with the help of new material. Work by Ewer (1965) and Krebs (1963, 1965) on *Euparkeria* and *Ticinosuchus* respectively, offers additional support to Hughes's conclusions. In the proterosuchians the foot anatomy is only known to an appropriate degree in *Chasmatosaurus* and *Erythrosuchus,* but it seems safe to infer that the condition in these genera was widespread among all the proterosuchians. The state is that of a tarsus without "crocodiloid" or "dinosaurian" specializations in the proximal tarsals (astragalus and calcaneum), and with a primitive, mesotarsal ankle joint. All other archosaurs show some type of tarsal modifications from this primitive condition, which is, by the way, like that in primitive lepidosaurians, such as *Youngina,* and in captorhinomorphs and pelycosaurs. All evidence indicates the convenience of placing this character-state in the *AN* class.

(22) The shape of the anterior spine of the iliac blade (Fig. 4) varies among the different proterosuchian genera from almost obsolete in *Chasmatosaurus* to moderately developed in genera like *Cuyosuchus,* but it is never highly developed, as it is in some pseudosuchians and "dinosaurs." The proterosuchian type of anterior spine of the ilium is very similar to that of the varanopsid pelycosaurs. At the same time, this same feature is also present in some non-proterosuchians, as is the case in *Euparkeria* and the rauisuchids, and for this reason it must be considered an *AS* character-state.

(23) The posterior spine of the iliac blade is long and narrow in all the known proterosuchian genera that afford evidence in this regard. Among the non-proterosuchian thecodonts, *Euparkeria* and the rauisuchids share the same condition, so

that this is also a character-state of the *AS* class.

(24) The fully closed condition of the acetabula is a proterosuchian character, associated with the amount of space between them; both conditions are related to the generally sprawled position of the posterior propodials. All the thecodonts show a closed acetabulum, and in most of them these are relatively far apart. Open and more closely approximated acetabula were developed in the saurischian and ornithischian dinosaurs in connection with the advanced bipedal stance. This is also an *AS* character-state.

(25) The relative length of the ventral pelvic bones varies within narrow limits in the proterosuchians, never reaching the development shown in more advanced archosaurs with triradiate pelves (Fig. 4). In the primitive forms the triradiate trend is only incipient, although it is more obvious in terminal forms like *Erythrosuchus*. In forms like *Chasmatosaurus* and *Cuyosuchus*, features of the very primitive puboischiadic plate can also be observed. *Euparkeria* shows in this respect a condition more proterosuchian than typically pseudosuchian, and *Ticinosuchus* seems to be transitional in this regard. This character-state must thus be considered to be in the *AS* class.

(26) Coracoids are known in *Chasmatosaurus, Cuyosuchus, Erythrosuchus, Shansisuchus* and *Vjushkovia*. In the first two they are obviously larger and more primitive than in the latter, but in any case, the proterosuchian coracoids are to be considered as large in comparison with those of most later archosaurs. Among the Pseudosuchia, large coracoids are present in *Euparkeria*, the rauisuchids *Ticinosuchus* and *Proterosuchus*, and the stagonolepidids. We must hence place this character-state in the *AS* class.

(27) The scapular blade is short and broad, and primitive in general shape, in both *Chasmatosaurus* and *Cuyosuchus* (Fig. 1). In the genera *Erythrosuchus, Shansisuchus*, and *Vjushkovia* it is higher and narrower, with both ends more expanded than the median "shaft." Short and broad scapulae are to be considered as primitive, and the shape of this bone in the erythrosuchids is obviously an improvement, which becomes more fully developed in pseudosuchians and later archosaurs. This character-state is to be placed in the *SN* set.

(28) The presence of dermal elements of the pectoral girdle is now known in *Chasmatosaurus, Shansisuchus, Erythrosuchus, Vjushkovia*, and *Cuyosuchus*. The first had been assumed to have a clavicle and interclavicle because of the presence of these bones in more advanced thecodonts (Hughes, 1963), but Young (1963) actually found a clavicle associated with other bones of *Chasmatosaurus yuani*. It is safe to conclude that dermal bones of the shoulder girdle were present in all the members of the Proterosuchia. At the same time, this primitive feature is also shared by many pseudosuchians, such as the rauisuchids, the stagonolepidids, *Euparkeria*, and even *Ornithosuchus* (see Walker, 1964: 110). We are dealing therefore, with a character-state of the *AS* class.

(29) As far as dermal armor is concerned, the Proterosuchia, in lacking any indication of it, are clearly different from all other thecodonts (Charig and Reig, in press). The only doubtful case in this respect is *Cuyosuchus*, as among the original material some atypical scutes were found. Since these could belong to the labyrinthodont found associated with the Argentinian proterosuchian, it is better not to consider this case as an actual exception. Crocodiles, phytosaurs, and ornithischians have osteoderms, but they are missing in saurischian dinosaurs (see below) and pterosaurs, so that the present condition must also be considered as an *AS* character-state.

Evolutionary and taxonomic significance of the proterosuchian character-states

The foregoing analysis indicates that the Proterosuchia-concept is not a fully polythetic one, as only five among twenty-nine peculiarities are not shared by all the members of its extension. But, by the same token, it is not a monothetic concept. More significant is the fact that eighteen of the twenty-nine character-states are shared by non-proterosuchian archosaurs. A completely phenetic classification, based on overall similarity, would indeed include some other taxa in the extension of the Proterosuchia-concept, a procedure that we believe would be misleading from the evolutionary point of view.

This analysis supports the inference that characters evolved at different rates in the early evolution of archosaurs. Some characters changed in state within the group Proterosuchia itself, as reflected by all characters in the *SN* set. In both cases of *SN* character-states, we are dealing with very primitive reptilian heritages, hardly to be considered of positive selective value at the archosaurian level of evolution, and their persistence should have been disadvantageous for the changes that the proterosuchians developed in skull architecture and locomotor improvements. Other characters changed only little beyond the proterosuchian threshold; they are our *AS* set. As in the former case, these are also primitive characters, most of which are maintained in some families of primitive pseudosuchians, in the first crocodiles, or in the phytosaurs, and only exceptionally in more advanced archosaurs. They seem to indicate that the achievement of a progressive archosaurian stage was, for more than half of the characters involved, a process of gradual evolutionary change. There are also those characters of our *SS* set that changed both within the proterosuchians and beyond them. They have the combined meaning of both the previous cases, and indicate that some proterosuchians evolved beyond the level reached by some of their first derivatives. These characters are useful, indeed, to infer phylogenies: no proterosuchian descendant can be supposed to have evolved from a proterosuchian ancestor that had evolved a different state in a character belonging to the SS class, if it maintains the same character in the state described in that class. There remains, finally, a set of characters that show little or no change within the Proterosuchia, but that behave differently beyond the proterosuchian threshold (the *AN* class). Nine of the twenty-nine analyzed belong to this group. In most of the cases, the change in these characters in proterosuchian descendants may be interpreted as improvements linked with the emergence of new evolutionary possibilities, as we will attempt to demonstrate below.

The general pattern of character-state changes within and beyond the proterosuchians is obviously indicative of the process known as mosaic evolution (de Beer, 1954), heterobathmy of characters (Takhtajian, 1959), or stepwise evolution (Bock, 1965 presents an illuminating analysis of the process).

As a matter of fact, characters involved in mosaic evolution do not afford any basis for a clear-cut distinction of a taxon from its close descendent relatives. In our case, this is especially obvious for the characters belonging to the *SN*, *AS*, and *SS* sets of character-states. On the other hand, character-states of the *AN* class actually do afford a clear-cut distinction of the Proterosuchia from the Pseudosuchia, the Crocodilia, the Parasuchia, and the other more advanced archosaurian groups. An Aristotelian-minded taxonomist would very easily find the clue for what in the context of his philosophy should be a mere pseudoproblem: he would choose only the *AN* character-states as the sufficient and necessary features that determine the "essence" of the Proterosuchia. This procedure will not satisfy the purposes of evolutionary taxonomy, as in this universe of discourse we are not trying to grasp the essence of any static entity, but to discover how to evaluate evolving characters in order to define evolving entities.

As far as the characters belonging to the *SN*, *AS*, and *SS* classes are concerned, the question could be raised whether they are not better excluded from the definition of the intension of the Proterosuchia-concept, as they are either shared by other non-proterosuchian archosaurs or not shared by all the proterosuchians. It could also be questioned whether the very existence of this kind of character-state is not an indication that the proterosuchian-concept is an artificial construct without any real referent in the objective world. We think that the answer to both questions must be negative, but in any case, it is true that we are facing a common and one of the most difficult of taxonomic problems: namely that of tracing borderlines (needed because of the requirements of taxonomy, but also, alas, because the human brain does not seem to be capable of functioning without categorizing) in ancestor-descendant series that evolve gradually from one state to the other. From the point of view of the logic of the system, an analysis of the "core" and the "fringe" of the taxonomic set represented by the proterosuchian-concept (as these terms have been defined and used by J. H. Woodger, 1952) would indeed help very much in a full elucidation of this problem. Such a sophisticated formal treatment is, however, beyond the aim of the present essay. We must keep in mind only that a fringe of vagueness seems to be unavoidable in any concept having evolving entities as referents; the peculiarities involved in such a vagueness are not to be excluded from the definition of this concept, if they are relevant for an adequate understanding of the evolutionary meaning of the entity we are dealing with. The polythetic nature of the proterosuchian-concept, with its fringe of vagueness, must be considered, on the contrary, an inherent quality of the concept, one which affords plenty of information for a better understanding of the features of early archosaurian evolution, a point which we will attempt to stress in the following part of this article.

But we must first refer to the following point: we have already said that Simpson and Gisin stressed the importance of alleged discontinuities arising during the process of detachment of a new taxon (as it shifts into a new adaptive zone) for the task of establishing non-arbitrary limits between major taxa. In Gisin's terms: "Um auch hier 'natürliche' Einheiten zu erhalten, müssen deren Grenzen den in der Natur objektiv gegebenen Diskontinuitäten, und diese einer bestimmten Qualität entsprechen" (Gisin, 1964: 9). These discontinuities given objectively in nature are believed to be the result of the threshold transition arising from a faster evolution between two major adaptive zones, a situation in which selective pressures act upon one character or a set of characters very strongly, making them evolve at a faster speed (the quantum effect). Should the explanation be correct, we would have a clue with which to trace borderlines between a series of ancestor-descendant major taxa, provided that we are able to discover which are the relevant characters involved in such a threshold effect, i.e., the "key innovations" responsible for the emergence of a new taxon. Whatever the relativity of the discontinuity, it should be possible to discover these characters if we have a complete enough fossil record.

The situation is perhaps less simple, however. Bock (1965) has contended that to postulate that in the origin of a major taxon (and hence in its delimitation) the operating process is a single-phase change, involving a switch from one major adaptive zone to another, implies an oversimplification not supported by any positive evidence. For him, the process is better thought of as a stepwise one, through which minor radiations occurred in the transitional adaptive zone. Key innovations and preadaptations are involved in this process, but there is no special reason to assume that evolution is greatly speeded up in the intermediate area. The stepwise character of the transition between major taxa is exemplified for Bock by the mosaic pattern of character changes occurring in the known cases of the emergence of major taxonomic groups. This view seems to discourage any attempt to look for natural boundaries between major taxa and, hence, to get an accurate assessment of the intension of their concepts.

It should be very interesting, therefore, to investigate just how the evidence from early archosaur evolution does match each of these views. But such an investigation will require, first of all, a new evaluation of the evidence, for the assessment we have made of the proterosuchian character-states will have new consequences for the explanation of the origin and early evolution of archosaurs. However, before discussing our main topic, we must refer to the origin of the proterosuchians, and to the proterosuchian descendants.

THE ORIGIN OF THE PROTEROSUCHIA

Obviously, if the Proterosuchia are the first and the most primitive archosaurs, the problem of the origin of the Proterosuchia is to be identified with the problem of the origin of the Archosauria. The latter has been considered a difficult matter and has been generally approached in a very broad context, usually in connection with the discussion of the alleged early split of the reptiles into two main branches, the Sauropsida and the Theropsida. A special account of this general question is beyond our present aim and we must restrict ourselves to the points more closely connected with archosaur ancestry [for a general survey of the whole matter, see Vaughn (1955), Watson (1954, 1957), Parrington (1958), Tatarinov (1959), Olson (1962)].

The fact that archosaurs and lepidosaurs have two-arched skulls led to their being grouped in one single taxon, the Diapsida, in early classifications. This taxon-concept has been generally abandoned since Romer (1956) advanced the current classification. But the general idea of a close relationship between archosaurs and lepidosaurs survives, and the concept of Diapsida is frequently used in phylogenetic discourse, although devoid of any explicit taxonomic intention. How close this relationship is is a matter of the disagreement, but little doubt has been cast upon the assumption that the two groups had a common origin, or that archosaurs are derived from early lepidosaurians.

The critical groups for the enquiry into archosaurian ancestry usually have been considered to be: the younginid eosuchians, the millerettiforms, and the captorhinomorph cotylosaurs. As far as the different possible hypotheses of archosaurian ancestry are connected with these three groups, we can speak of the younginid hypothesis, the millerettiform hypothesis, and the captorhinomorph hypothesis.

In a recent paper (Reig, 1967), I have briefly discussed these different hypotheses, pointing out that the proterosuchian character-states make it necessary to rule out both the younginid and the millerettiform hypotheses. Each of these groups is more advanced than the first archosaurs (the proterosuchians) in relevant character-states.

The younginid hypothesis was first advanced by Broom (1914, 1922, 1924a, 1946) and has been subsequently adopted by such authors as Camp (1945), Piveteau (1955) and von Huene (1956). This hypothesis maintains that the archosaurs, the rhynchocephalians, and the squamates took their origin from the younginids, represented by the small South African *Cistecephalus* Zone reptiles *Youngina, Youngoides,* and *Youngopsis,* known mostly from skull material. The family Younginidae forms the central group of the suborder Younginiformes of the Lepidosauria in Romer's (1956) classification, the other families of the same suborder being Paliguanidae, Prolacertidae, and Tangasauridae. The younginids have both the diapsidan temporal opening fully developed (character-state i of our *AA* class) and the typical lepidosaurian otic notch, formed by a curved posterior border of the quadrate and defined above by a small spur of the squamosal (in disagreement with our proterosuchian character-state 4). At the same time, the suspensorium is nearly at the same level with the occipital region (contradicting our character-state 6), and the quadrate is attached by suture with the squamosal in a monimostylic way (in contrast with character-state vi of our *AA* class).

It is now generally accepted that the younginids can be considered as the stem group of the Rhynchocephalia and that the origin of the Squamata is better sought in the Prolacertidae (Camp, 1945; Parrington 1935; Kuhn-Schnyder, 1954, 1962). As far as the archosaurs are concerned, the younginid ancestry has been seriously questioned by Romer (1946, 1956). And apart from the arguments of this author, it is clear that the younginids cannot be considered ancestors of the proterosuchians because of the structure of the quadrate, as even the first proterosuchians (i.e., *Chasmatosaurus*, Brink, 1955) show a movable quadrate, articulated with the squamosal through a head, a condition which has been established in the millerettids (Watson, 1957). But in addition, the lack of any sort of otic notch and the very backward position of the mandibular articulation of the quadrate (shown already in the most primitive proterosuchians) definitely preclude the idea of any kind of younginiform ancestry for them. The proterosuchian character-states 4 and 6 constitute a serious objection to the younginid hypothesis, and this is better abandoned.

The core of the Millerettiformes (also a suborder of the Eosuchia of the Lepidosauria in Romer's classification of 1956) is formed by several genera described by Broom (1938, 1940, 1948) from the same *Cistecephalus* beds of South Africa and placed in the family Millerettidae. Earlier genera of the same group are usually referred to different families. The whole taxon has been carefully surveyed by Watson (1957) who maintained that these are sauropsid reptiles possessing very primitive qualities, though not having already developed the two-arched condition. He suggested (1957: 388) that the thecodonts could have come direct from the Millerettiformes (called by him Millerosauria), and, in the chart of figure 23 of the same work, he derives the Pseudosuchia plus later archosaurs and the "Erythrosuchia" (= Proterosuchia), as a separate branch, from the "millerosaurs." The implication is that the proterosuchians do not belong in the ancestry of later archosaurs (a contention not expressed in his text), but that both pseudosuchians and proterosuchians evolved independently from "millerosaurs." As we shall make more evident below, no relevant evidence exists ruling out the proterosuchians from the ancestry of the pseudosuchians and, on the contrary, the presence of such intermediate forms as *Euparkeria* suggests that proterosuchians actually were the ancestors of the pseudosuchians.

As far as proterosuchian origin from the millerettids is concerned, it is highly improbable that at least any of the small genera of the *Cistecephalus* Zone could be in the line of proterosuchians. All of them have an otic notch already developed, and the quadrate in an upright position, with the mandibular articulation close to the occipital plane. These are character-states that are not expected to be found in any proterosuchian ancestor. It is true that the millerettids are more plausible archosaur ancestors than are the younginids, because the former have a movable quadrate-squamosal articulation, but, at the same time, the millerettids had not reached the diapsid condition already developed in the younginids. Furthermore, the millerettids could hardly be considered as adequate forerunners of the contemporaneous *Archosaurus* from the Russian Upper Permian Zone IV. This genus indicates that, at the time the millerettids thrived, the proterosuchids were fairly large animals which had already developed their typical character-states.

However, discarding the millerettids as direct proterosuchian ancestors is not the same as discarding the millerettiform hypothesis, since the group is not restricted to millerettids of the South African *Cistecephalus* Zone. The older *Tapinocephalus* Zone of the Karroo succession has yielded *Broomia*, a genus tentatively placed in a family of its own, and the still older strata of the Mesen River in Russia (Upper Kazanian, Zone II of the Russian Permian) afforded *Mesenosaurus*, a genus considered of pelycosaur affinity by Efremov (1938) and by Romer and Price (1940), but more correctly placed in the Millerettiformes as the type of a family of its own (Watson, 1957; Romer, 1956; Tatarinov, 1964). Romer (1967) has stressed the phylogenetic importance of the Millerettiformes. They are likely to have been a widespread group, both in time and in space. Can it be supposed, therefore, that the Proterosuchia evolved from some early millerettiform population? This is hardly probable, as such an early member of this taxon as *Mesenosaurus* had already acquired, according to published descriptions, a perfect otic notch. The Millerettiformes are better considered as forerunners of the Lepidosauria, not as a group having direct relationships with the archosaurs.

Romer (1956: 519) suggested that the archosaurs might have arisen independently from cotylosaur ancestors. It is obvious that the captorhinomorphs are here implied, as he did not consider other cotylosaur groups as being close to the archosaurs. The two-arched temporal region of archosaurs and lepidosaurs would in this view be another case of parallelism, which, by the way, might also be the case if one advocated a millerettiform ancestry.

The first adequately known captorhinomorph, and also the earliest adequately known reptile, comes from the Lower Pennsylvanian (Westphalian A) of the Port Hood formation in Nova Scotia. This is the genus *Romeriscus*, a limnoscelid recently reported by Baird and Carroll (1967). Remains of two romeriid captorhinomorphs and one pelycosaur have also been described from the Joggins of Nova Scotia, a slightly higher level in the Lower Pennsylvanian (Westphalian B) (Carroll, 1964). Romeriids are represented also by dubious remains from the Middle Pennsylvanian, and they are better known through their last representatives in the Lower Permian (*Romeria*, *Protorothyris*). The other captorhinomorph family, namely the captorhinids, has its first members in the Lower Permian Leonardian stage (see Table I), with *Captorhinus* as a well-known representative. Members of this family are, moreover, the latest captorhinomorphs, reaching the early Guadalupean and early Kazanian (*Rothia*, *Kahneria*, etc.). The limnoscelids departed very early from the main line of reptilian evolution (Baird and Carroll, 1967), so that only romeriids and captorhinids could be relevant in the discussion of archosaur ancestry.

It is clear that both romeriids and captorhinids would make better archosaur ancestors than younginids, prolacertids, or millerettids, in the sense that they do not contradict the requirement of the absence of an otic notch as demanded by the proterosuchians. They are, however, very archaic, fully anapsid, and with the suspensorium not primarily posterior in position. The form and the relationships of the quadrate, moreover, are more archosaur-like in the millerettids than in the captorhinomorphs. However, Parrington (1958) has demonstrated that the millerettid condition of the quadrate is easily derived from that of *Captorhinus*. But, as the same arguments used by Parrington

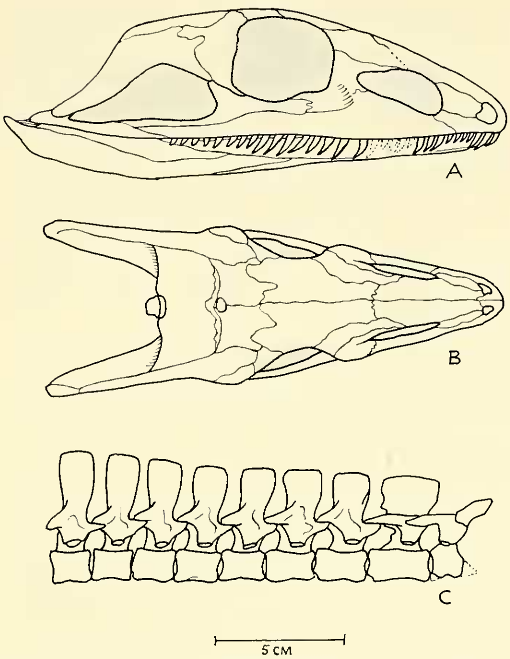

Figure 6. *Varanodon agilis* Olson. A, lateral view of the skull; B, dorsal view of the skull; C, series of cervical vertebrae. (From Olson.)

could be applied to derive the archosaurian condition of the quadrate from that of the captorhinids, this does not run counter to the possibility of captorhinomorph derivation of the archosaurian skull. In fact, no theoretical objection can be raised against the contention that the proterosuchian skull, diapsid, without otic notch, and with a very posterior suspensorium could be derived from a romeriid or captorhinid skull. Furthermore, the postcranial skeleton is so primitive in these cotylosaurs that practically every proterosuchian character-state of that part of the body could easily be thought of as having evolved from a captorhinomorph state.

But it is clear that too large a morphological gap exists between even the more primitive proterosuchians and the more advanced captorhinomorphs, and neither romeriids nor captorhinids show any definite trend towards some of the peculiar archosaurian character-states. Even if intermediate forms should be discovered between captorhinomorphs and early archosaurs, the amount of difference between the ancestor and the descendent groups would necessarily be so great that the linking group might better be considered as a major taxon of its own. In this case, the captorhinomorph hypothesis should be transformed into one arguing for ancestry from this intermediate taxon.

Another objection to the captorhinomorph hypothesis is the lack of explanatory value, as it can be agreed that many reptilian groups could eventually have stemmed from captorhinids or romeriids. Moreover, it becomes clear that this hypothesis should be abandoned if another reptilian group more closely related to the first archosaurs exists. As I have already proposed (Reig, 1967), I believe that a strong case exists for assigning this role to a definite group of pelycosaurs; this makes it necessary to put forward a new hypothesis, namely the pelycosaurian hypothesis.

This idea is not completely new. The notion of pelycosaur and archosaur relationships was first expressed by von Huene (1911), when he discussed the position of *Erythrosuchus*. He found that this genus shared with pelycosaurs so many features in skull and postcranial morphology, that he created for it an order of its own, Pelycosimia, a name coined with the evident purpose of expressing the idea of pelycosaur relationships. He later abandoned the idea of the Pelycosimia as a separate order, and the name has been used in its original spelling, or as Pelycosimioidea, as an equivalent of Proterosuchia, or Proterosuchoidea, and, hence, as a taxon subordinated in the Thecodontia.

More recently, Rozhdestvenskii (1964: 204) suggested plainly the pelycosaur origin of the archosaurs, when he said: "The mammal-like reptiles, and particularly the pelycosaurs, are also to be considered as archosaur ancestors. The earliest archosaurs, the Triassic thecodonts, are

Major Divisions		Standard American Scale		North-Central Texas		Standard Russian Stages	Russian Continental Zones	Karroo System in South Africa		Position of Genera Relevant to the Problem of the Ancestry of Archosaurs
PERMIAN	UPPER PERMIAN	OCHOAN SERIES				TATARIAN (?)	IV	CISTECEPHALUS: B	LOWER BEAUFORT STAGE	ARCHOSAURUS; HOMODONTOSAURUS; YOUNGINA, YOUNGOPSIS, YOUNGOIDES; MILLERETTIDS
		GUADALUPIAN SERIES	CAPITAN	WHITE HORSE GROUP (?)		TATARIAN	IV	CISTECEPHALUS: A		"PROBLEMATIC REPTILE" OF PARRINGTON
			CAPITAN	WHITE HORSE GROUP		TATARIAN	III	ENDOTHIODON		
			WORD	PEASE RIVER GROUP	DOG CREEK	KAZANIAN	II	TAPINOCEPHALUS		BROOMIA; ELLIOTSMITHIA, ANNINGIA
					BLAINE					
					FLOWERPOT SHALE	UFIMIAN		ECCA SERIES		MESENOSAURUS; VARANODON; ROTHIA, KAHNERIA
					SAN ANGELO		I			
	LOWER PERMIAN	LEONARDIAN SERIES		CLEAR FORK GROUP	CHOZA	KUNGURIAN	I			
					VALE					
					ARROYO	ARTINSKIAN	O			VARANOSAURUS; VARANOPS
				WICHITA GROUP	LUEDERS			ECCA SERIES / DWYKA SERIES (?)		AEROSAURUS, SCOLIOMUS; OPHIACODON
					CLYDE					
					BELLE PLAINS					
		WOLFCAMPIAN SERIES			ADMIRAL	SAKMARIAN		DWYKA SERIES		VARANOSAURUS; OPHIACODON
					PUTNAM					
					MORAN					
					PUEBLO					

Table I. Correlation Chart of the Various Divisions of the Permian in U.S.A., South Africa, and Russia. (Mainly from Dunbar and from Olson.)

significantly similar to the pelycosaurs, both in general features and in details."

The pelycosaurs are, however, a large group including several specialized subordinate taxa that are surely not connected with the archosaurs. The more generalized members of this order are to be sought in the Ophiacodontia and in the Varanopsidae among the Sphenacodontia. Even though some ophiacodontids show several notable resemblances to the more primitive proterosuchians, this is not the group most likely to include the archosaur ancestors. It is the varanopsids that have features that strongly suggest proterosuchian relationships, and that have developed some character-states that are found elsewhere only in the archosaurs among the reptiles. Olson (1965) has recently described *Varanodon agilis* (Fig. 6), an advanced varanopsid from the Guadalupean of Oklahoma, which strongly suggests a theoretical proterosuchid ancestor in skull and postcranial structure. It is thus desirable to consider the composition of this family.

The best known genus of the Varanopsidae is *Varanops*, from the Clear Fork beds of Texas (Leonardian, Lower Permian: see Table I to visualize the Permian successions), carefully described by Romer and Price (1940). These authors referred to the same family the genera *Aerosaurus* and *Scoliomus*, from the largely equivalent Abo beds of New Mexico, the South African *Elliotsmithia* and *Anningia* (= *Galesphyrus*) from the *Tapinocephalus* Zone of the Upper Permian, and the Russian *Mesenosaurus*, which, as has already been said, is now better placed in the Millerettiformes. *Homodontosaurus* of the South African *Cistecephalus* Zone has also been included in the same family. However, the position of the South African and New Mexican genera is doubtful. Watson (1957) suggested that *Elliotsmithia* and *Anningia* might be considered to be millerettids; *Aerosaurus* and *Scoliomus* are known from material too fragmentary to permit an accurate family allocation. *Homodontosaurus*, a pelycosaur according to Broom (1949), is considered a therapsid by Brink (1950), and the nature of the material suggests that it is better considered as a synapsid *incertae sedis*. Olson (1965) maintains that *Varanops* and his new genus *Varanodon* (Fig. 6) are the only genera to be considered as certainly belonging to this family, and, as far as the other genera are concerned, in his view *Elliotsmithia* is the only one for which a convincing case can be made.

Extending from the lowest Vale (*Varanops*) to the *Tapinocephalus* Zone, the family Varanopsidae would be a long-lived one during Permian times, and its extension in time matches very well that which would be expected for a group ancestral to the archosaurs.

The skulls of varanopsids and ophiacodonts share a number of characters with the proterosuchians. First of all, the absence of an otic notch, the presence of a lateral temporal fenestra, and the posteriorly situated suspensorium with the quadrate strongly slanting backwards, constitute an assemblage of characters that we have not found associated in any of the other groups alleged to be connected with archosaur ancestry; by themselves these make a strong case for suggesting relationships. Besides this, there is the common possession of postparietal and postfrontal bones and of a pineal foramen, conditions that even though not indicative of special relationships, for the same character-states are shared by other primitive reptiles, do not contradict our hypothesis. Far more important is the fact that so typical an archosaur character-state as the presence of an antorbital fenestra has been described in *Varanodon* and is apparently also present in *Varanops* (Olson, 1965). At the same time, the characteristic archosaur mandibular fenestra is found well developed in *Ophiacodon* (Romer and Price, 1940) and apparently also in *Varanops* (a detailed account of the mandible of *Varanodon* has not yet been reported). Moreover, ophiacodontids and varanopsids share with the proterosuchians an elongated antorbital region, an occipital plane that is concave and slants forward towards the skull table (as in most pelycosaurs), and large prefrontal bones that project laterally and form a ridge, making an abrupt limit between the roof of the skull in front of the orbits and the lateral antorbital region. The palate is not adequately known in the Varanopsidae, but typical proterosuchian character-states, such as pterygoid flanges, teeth on these flanges, and long and narrow interpterygoid vacuities, are observable in *Ophiacodon*. Pelycosaurs also have in common with the proterosuchians and some later archosaurs the presence of epipterygoids and the small size of the posttemporal fenestra, and in both groups the prootics are extensive. A peculiar condition of the pelycosaurs is the presence of a prominent *dorsum sellae* formed mainly by the prootics, rather than by the basisphenoid (Romer and Price, 1940; Romer, 1956). This condition is not known in the proterosuchians, but the fact that in the phytosaurs the *dorsum sellae* is partly formed by the median union of the prootics (Camp, 1930), suggests that participation of the prootics in the *dorsum sellae* is to be expected in proterosuchians.

The proterosuchian skull is metakinetic (Versluys, 1910: 197), and this seems also to be the original condition of the pelycosaurs (Versluys, 1912: 661). As far as skull kinetism is concerned, however, an important difference between the pelycosaurs as a whole and the proterosuchians is the nature of the quadrate, which is completely monimostylic in the former and streptostylic in the latter. It is clear, nevertheless, that more research is needed in order to know which is the primitive condition of this character. We have already mentioned that the movable quadrate of the millerettids seems to be easily derivable from the rigid condition of *Captorhinus* (Parrington, 1958).

Additional differences are shown in the fact that all pelycosaurs lack the upper temporal fenestra and that they retain the tabular and supratemporal bones and have not developed laterosphenoid ossifications. All these character-states are, however, to be expected in proterosuchian ancestors, the different state in the first archosaurs being obviously an evolution from a primitive condition like that seen in the pelycosaurs or romeriid captorhinomorphs. Romer and Price (1940: 194–195) argued that the diapsid condition of the archosaurian skull is hardly derivable from the synapsid condition of the pelycosaurs. Their arguments, however, do not seem to the present author very convincing, and there seems to be no serious doubt that, as Kuhn-Schnyder recently advocated (1962), the development of the lower temporal fenestra is the first step towards the realization of the two-arched, diapsid condition. The size and position of the temporal fenestra in the Varanopsidae make it clear that this fenestra is homologous with the diapsidan lower temporal fenestra. Another point against pelycosaur-archosaur relationships in the Romer and Price argument, the morphology of the pelycosaur occiput, is contested by present knowledge of occipital structure in the proterosuchians.

Another distinction refers to the anterior extensions of the lacrimals that in ophiacodontids and varanopsids contribute to the borders of the external nares. This feature is not shown by any proterosuchian, but the fact that the same condition is observed in other primitive groups, such as millerettids, diadectids, gephyrostegids, and captorhinomorphs, suggests that this is a primitive reptilian heritage; it is not surprising to find it in proterosuchian ancestors.

Taking into account the combined group of the ophiacodonts and varanopsids, it is highly suggestive that they share four of the eight character-states of *AA* class (2, 3, 5, 8) that refer to skull characters, and that in one other (1) they are intermediate. Even more suggestive is the fact that they share all the thirteen skull character-states of the proterosuchians (character-states 1–13 of our list). In short, the data of skull anatomy seem to indicate that the primitive pelycosaurs of the ophiacodontid-varanopsid group make better proterosuchian (and archosaur) ancestors than any other reptilian group. Among these, the Varanopsidae show character-states suggesting that they are close to the group from which the proterosuchians may have arisen, as they have already developed the otherwise characteristically archosaurian antorbital fenestra and have a very large lateral temporal opening and strongly backward-oriented suspensorium.

The same conclusion is supported by the axial skeleton. The pelycosaurian vertebral column is of course more primitive than the proterosuchian one, as the vertebrae have persistently notochordal centra, intercentra commonly present in all the presacral vertebrae, and a presacral number of twenty-seven. The vertebral morphology, however, does not preclude archosaur ancestry in any way. On the contrary, proterosuchian vertebrae show character-states such as the presence of lamellae connecting the apophyses for the rib heads (present also in ophiacodonts, at least) that seem to be reminiscent of the primitive pelycosaur condition. The atlas-axis complex is closely comparable in *Chasmatosaurus* and the ophiacodonts, as Broili and Schroeder have already pointed out (1934), and the Varanopsidae (Fig. 6c) add to the general picture the fact that they have, as in the primitive proterosuchians, elongated cervical centra (Romer and Price, 1940: 274; Olson, 1965: 53) and a tendency for the dorsal rib facets to become more closely approximated from the front backwards. The similarity in sacral vertebrae is also striking, as von Huene (1911: 36) noted, and this similarity becomes more evident when primitive pelycosaurs are considered, as both ophiacodontids and varanopsids have only two sacral ribs. Mention should also be made here of the few vertebrae associated with portions of humerus and ulna and other fragments that Parrington (1956) described from the Upper Permian (*Endothiodon* Zone) of Tanganyika. The vertebrae of this "problematic reptile" are suggestive of a transitional type between pelycosaur and archosaur vertebrae; they are pelycosaurian in the retention of the notochordal canal, and archosaurian in the form and position of rib articulations. It is of interest to note that these remains come from a level in the Upper Permian immediately following the *Tapinocephalus* Zone, which yielded the specimens of the supposed last varanopsid, *Elliotsmithia*.

Of prime interest for the pelycosaur hypothesis are the striking resemblances that exist in the morphology of the appendicular skeleton between proterosuchians, on the one hand, and ophiacodontids and varanopsids, on the other. Members of both these pelycosaurian families show the primitive reptilian feature of sprawled legs, as in the proterosuchians (character-state 16), and both are, of course, quadrupedal (character-state 15). But, at the same time, ophiacodontids and varanopsids present the characteristic archosaurian limb disparity (character-state xiii of the *AA* class) in just the stage of development shown by the proterosuchians (character-state 17). The girdles and the limbs show striking points of affinity, even in details. The scapular blade in *Chasmatosaurus* and *Cuyosuchus* is closely comparable to that in *Ophiacodon* and *Varanops*: short and broad by archosaurian standards, with a supraglenoid buttress and a supraglenoid foramen (at least in *Cuyosuchus*) (Fig. 7). This character-state (27) is not shared by all proterosuchians, as has already been said, and it is interesting that such a feature of the *SN* class should be shared by varanopsids and ophiacodontids. As far as the coracoids are concerned, pelycosaurs differ strongly from archosaurs in the possession of two coracoidal ossifications, a point that has been stressed by Romer and Price (1940: 194) in discarding the possibility of pelycosaur-archosaur relationships. But it is now commonly agreed that the single archosaur coracoid represents the synapsid precoracoid, and the presence of two coracoids in various primitive reptiles (such as pelycosaurs, captorhinids, procolophonoids, and pareiasaurs) proves that two coracoidal ossifications are an early acquisition in the first reptiles, and that this condition has been lost in later stages of reptilian evolution, the synapsids being the only group in which it survived. From this assumption, it is logical to conclude that in the ancestors of archosaurs a trend towards the reduction or disappearance of the posterior "true" coracoid occurred. It is therefore highly significant that among the Varanopsidae, which show

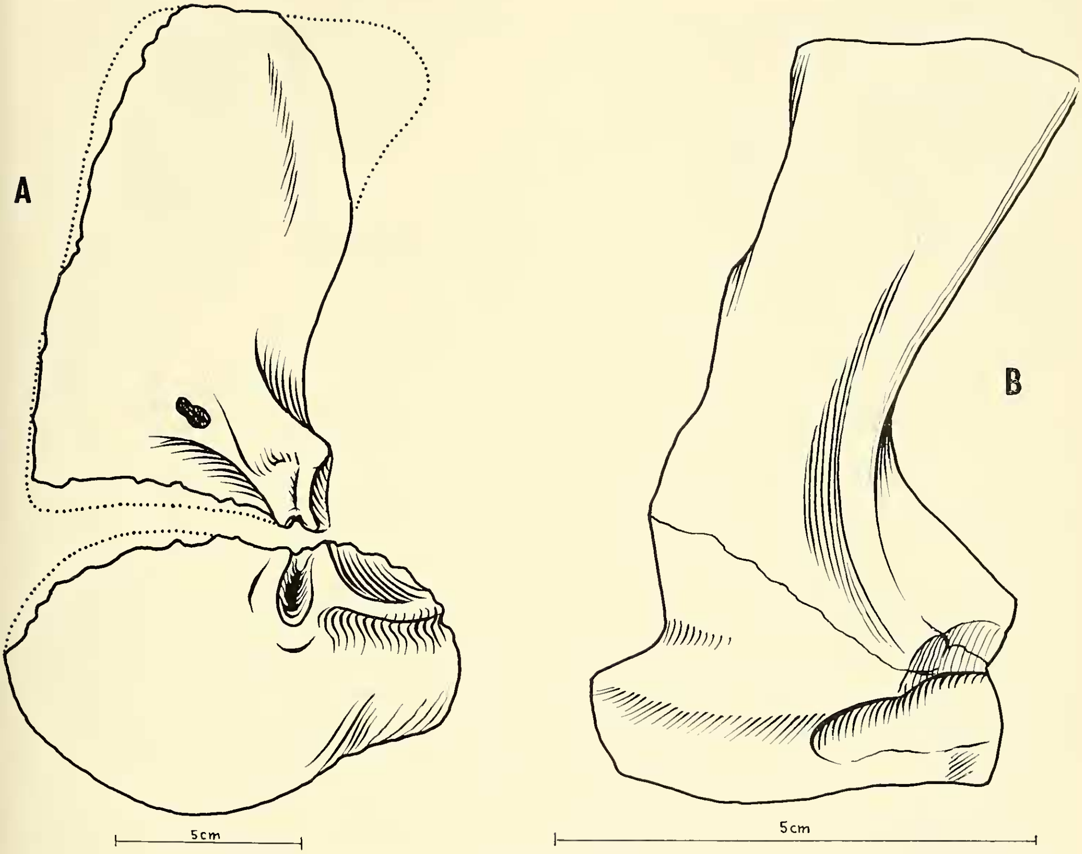

Figure 7. Scapula and coracoid of one proterosuchian and one varanopsid pelycosaur. A, *Cuyasuchus huenei* Reig; B, *Varanops brevirostris* (Williston). (A, from original specimen; B, from Romer and Price.)

so many similarities to the proterosuchians, *Varanops* (Fig. 7) is unique among pelycosaurs in lacking a posterior coracoidal ossification (Williston, 1914)—a feature that has been interpreted by Romer and Price (1940: 274) as a lag in ossification; this lag has been reported by the same authors (1940: 263) as a characteristic feature in sphenacodonts. The situation in other typical varanopsids is not clear in this respect, and the ophiacodonts exhibit the characteristic double condition of the pelycosaurian coracoids.

In pelycosaurs, the humerus is characterized by the expanded and twisted ends, the distinct shaft region, the presence of a large entepicondylar foramen, and a well-developed deltopectoral crest. The known humeri of proterosuchians, with the exception of *Cuyosuchus,* also possess expanded and twisted ends (character-state 20), a strong deltopectoral crest, and distinct shaft. They look very different from the humeri of most of the pseudosuchians and are very close to the pelycosaurian ones, but they do not show the entepicondylar foramen characteristic of the latter. However, it must be noted that the humerus of *Chasmatosaurus* recently figured by Young (1963) is not only closely comparable with that of *Varanops,* but also shows a discontinuity in the entepicondylar border in

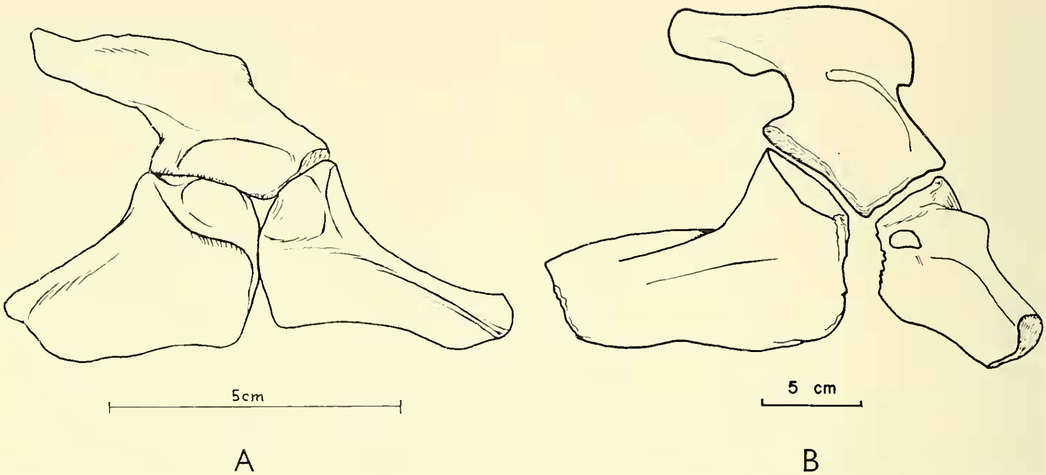

Figure 8. Pelves of one varanopsid pelycosaur and one proterosuchian thecodont. A, *Varanops brevirostris* (Williston) (from Romer and Price); B, *Vjushkovia triplicostata* von Huene (from von Huene).

the position where the entepicondylar foramen should be placed, which suggests that such a foramen might be present in this genus, its external bridge of bone being broken in the specimen. An ectepicondylar notch is also evident.

The anterior epipodials are short and subequal in size both in pelycosaurs and proterosuchians. The former have a well-developed olecranon on the ulna, which is apparently lacking in the proterosuchians. But, as Romer and Price have indicated (1940: 46), the extreme lag in ossification of the olecranon during ontogeny makes this character untrustworthy in problems of phylogeny. It is suggestive that the ulna of *Varanops* looks very much like that of *Chasmatosaurus* described and figured by Young (1936), especially as regards the proximal end, which in both is massive and has a relatively weakly developed olecranon area.

We have already said that the pelvic girdle of the primitive proterosuchians may be better described as incipiently triradiate, the triradiate condition being more evident in such advanced forms as *Erythrosuchus*. Earlier forms retain many primitive characteristics, such as a reduced but fairly continuous puboischiadic plate. The pubis in *Varanops* (Fig. 8) has a very strong upper border directed forwards and downwards, and can be described as a twisted plate of bone, as is the case in the proterosuchians. The ischium also shows a strong upper border directed backwards and downwards, and the puboischiadic plate is reduced. These features are closely comparable to those in primitive proterosuchians and suggests that the archosaurian trend toward a triradiate pelvis was beginning to develop in *Varanops*-like pelycosaurs. This corresponds to our proterosuchian character-state 25. As far as the other pelvic characters are concerned, the ilia of *Chasmatosaurus* and *Shansisuchus* are very like that of *Varanops* in that the anterior process of the blade is very weakly developed (character-state 22). This process is absent in the ophiacodonts, but is very well developed in later sphenacodonts and edaphosaurs. The posterior spine of the blade is long and narrow in ophiacodonts and more proterosuchian-like in *Varanops*. In short, the ilia of varanopsids and proterosuchians are very similar, which is not the case in more advanced pelycosaurs.

The femur of proterosuchians has been reported as being very primitive in that it possesses a terminal head, an intertrochanteric fossa, and an internal trochanter (character-states 18, 19). These features are characteristically present in the pelycosaurs. In pelycosaurs, however, the posterior condyle is far larger than the anterior one, as is clearly shown in advanced sphenacodonts and in edaphosaurs. In the proterosuchians, this characteristic is not noticeable, and it is again strongly significant that this condylar disparity is far less marked in *Varanops* and in the ophiacodontid *Varanosaurus* than in the typical pelycosaurs. The femur of *Chasmatosaurus* figured by Young (1963) looks very like that of *Varanops* in this respect and also in general shape.

The posterior epipodials are generalized in both pelycosaurs and proterosuchians, and do not afford any evidence of relationships. As far as the foot is concerned, in both groups the astragalus and calcaneum are large elements, closely appressed one to the other and to the fibula and tibia, so that most of the ankle joint is mesotarsal (character-state 21). In addition, the metatarsals of *Chasmatosaurus* (Young, 1936, fig. 12) are very like those of *Varanosaurus* and *Varanops* in general shape and proportions. In the three genera, the fourth metatarsal is the largest, and the size progression is the same: $1<2<5<3<4$. The phalangeal formula of *Chasmatosaurus*, as restored by Young, is, as in pelycosaurs, the primitive reptilian one, with the improbable exception of the three phalanges of the first toe, which is almost surely a faulty reconstruction.

We should finally mention that an additional point of resemblance is afforded by the dichocephalous type of ribs, a characteristic archosaur feature (character-state x of our *AA* class) that is shared by ophiacodontids, varanopsids, and most of the other pelycosaurian groups, and that pelycosaurs also agree with the proterosuchians in the presence of a dermal pectoral girdle (character-state 28) and the absence of dermal armor (character-state 29).

As in the case of the skull characters, an analysis of the traits of the postcranial skeleton affords an overwhelming array of similarities between the proterosuchians and the ophiacodontid-varanopsid group. Both groups share three of the five character-states of our *AA* class and practically the whole set of the sixteen postcranial character-states we have listed for the proterosuchians. Obviously, these figures could be misleading, as they do not cover important dissimilarities that we have pointed out in the text. But, as we have already discussed, these dissimilarities do not preclude in any case the possibility of the pelycosaur hypothesis, the proterosuchian state of the pertinent characters being readily derivable from the pelycosaurian state. What they indicate is that the group of pelycosaurs in question has not reached the proterosuchian stage of evolution in several relevant features, a conclusion that does not contradict our hypothesis, since it is not here intended to demonstrate that these pelycosaurs *are* proterosuchians, but only that they include the taxon from which the proterosuchians could have taken their origin.

As in the case of the skull characters, we have also observed that within the ophiacodontid-varanopsid group of pelycosaurs, the Varanopsidae seem to be plainly in the line of archosaur ancestry, as they have already developed, or begun to exhibit, relevant trends toward the first archosaurs, such as the single nature of the coracoid, the general shape of the pelvis, the elongated cervical centra, and the pattern of the rib facet displacement in the dorsal vertebrae. None of these trends is developed in more advanced pelycosaurs, and when we also recall that the archosaurian features already developed in the varanopsid skull, such as the antorbital fenestra, the large lower temporal opening, the probable presence of a mandibular fenestra and the backward displacement of

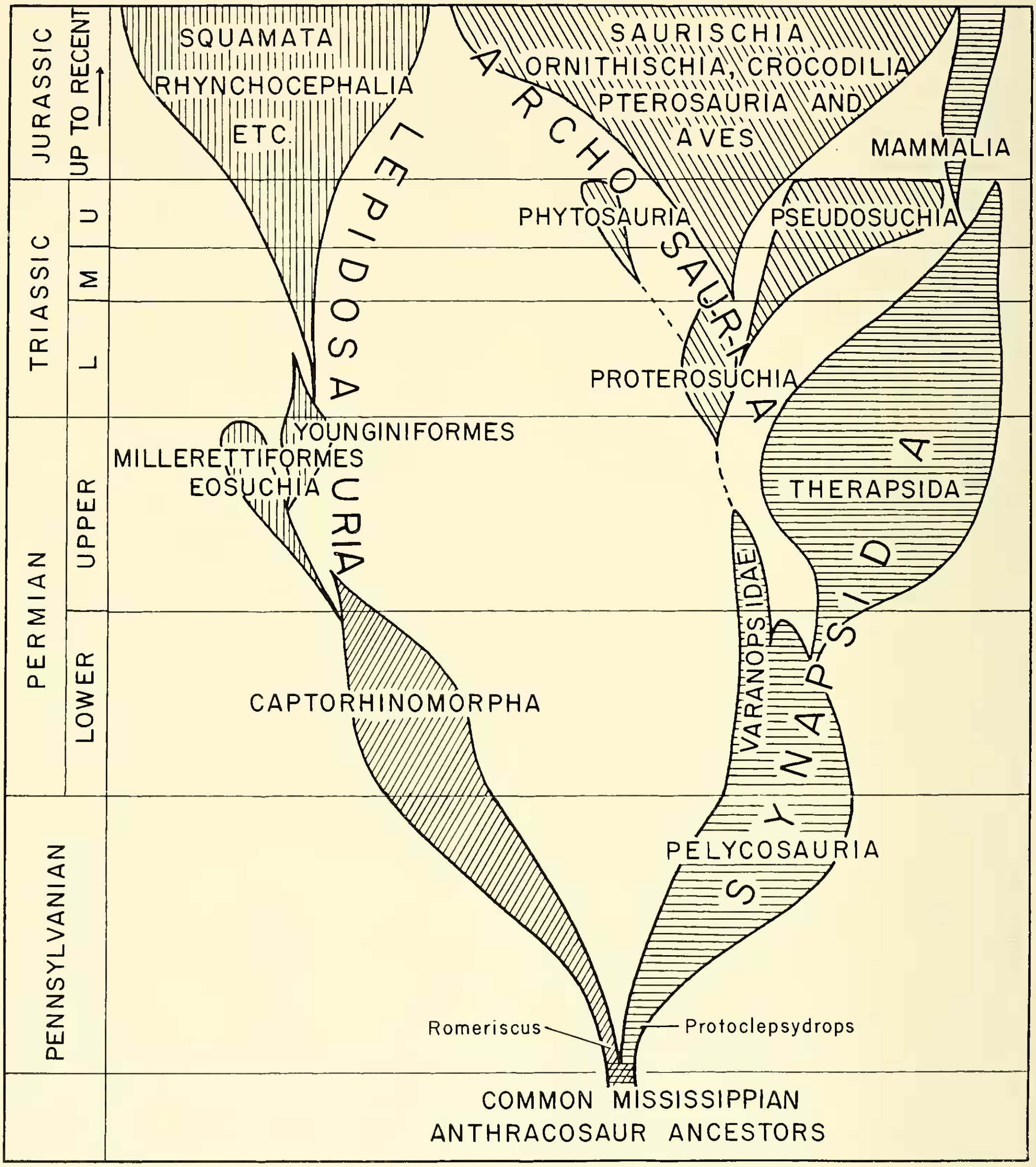

Figure 9. Phylogenetic diagram of the suggested ancestry of the Archosauria and the probable relationships among captorhinomorphs, synapsids, lepidosaurs and archosaurs. (Modified from Reig, 1967.)

the mandibular articulation, are not developed in the more advanced pelycosaurs, we can agree with Olson's suggestion that the Varanopsidae have departed from the main lines of pelycosaur evolution (Olson, 1965). Romer and Price (1940), however, maintained that the Varanopsidae are ancestral sphenacodontians, a contention that does not seem to be supported by the specialized, archosaur-like features shown by the known members of this family. The occurrence of true sphenacodonts as early as the Lower Pennsylvanian (Carroll, 1964; Baird and Carroll, 1967) clearly indicates, moreover, that the hypothesis of derivation of sphenacodontids from varanopsids should be at least submitted to a critical reappraisal. In our present state of knowledge, I think it is more reasonable to place the Varanopsidae in the Ophiacodontia, as a family in which at least the known members separated from the main direction of synapsid evolution to follow their own evolutionary course, a course that eventually led to their transformation into the proterosuchians. The possibility should not be discarded, however, that very early, unknown varanopsids could be the common ancestors of both sphenacodontians and proterosuchians.

Mention must also be made here of the problematic late Pennsylvanian reptile *Petrolacosaurus* (Peabody, 1952). On the basis of strong similarities in the palatal structure with the eosuchian *Youngoides* and rather less relevant postcranial features, Peabody interpreted this genus as being a primitive eosuchian and proposed a diapsid reconstruction of its skull. This reconstruction is obviously quite hypothetical, but the material seems to suggest, at least, that it possessed a lower temporal opening. Analyzing the quadrate region of the skull and other cranial features, Watson (1954) contended that *Petrolacosaurus* is to be considered a theropsid reptile, a contention that Vaughn (1955) is inclined to accept. In agreement with these views, Romer (1966b) places *Petrolacosaurus* as a probable member of the primitive edaphosaurian family Nitosauridae. It seems to me highly probable that this genus belongs to the Pelycosauria, the data afforded by Peabody giving strong support to this interpretation. If this is the case, it must be noted that the structure of the palate and the elongated cervical centra shown by *Petrolacosaurus* are character-states suggestive of archosaurian ancestry. But in other respects, this genus is so primitive that it cannot successfully contend with the known varanopsids as a proterosuchian ancestor, the geological occurrence of the varanopsids being also more consistent with the idea that they make better forebears of the archosaurs.

I believe that the body of evidence supporting the pelycosaurian hypothesis (Fig. 9) is stronger by far than that supporting any alternative view, and I have not been able to find any serious evidence against it. Apart from its empirical foundations, it can also be said that the hypothesis is also supported by such attributes as explanatory value and simplicity. It is able both to explain the until now obscure question of archosaurian origin in a simple way, and also to explain the reasons for seemingly aberrant features of the late Varanopsidae and the peculiar characteristics of the proterosuchians. It is also rich in suggestions that explain the ecological factors underlying early archosaurian evolution, and is in agreement with other cases of emergence of major groups, namely a pattern of steady development of features of the evolving group.

ECOLOGICAL AND EVOLUTIONARY FEATURES WITHIN THE PROTEROSUCHIA

We have already suggested in the introduction that the proterosuchians represent the first step in an exploratory radiation performed by the thecodonts before the complete dominance of the archosaurs at the end of the Triassic. Now, it will be of prime interest to investigate what conclusions can be drawn about the pattern followed by early archosaurian evolution during this first phase. For this, knowledge of the ways of life and the ecological roles of the proterosuchians can afford important data.

Not much doubt can be cast upon the conclusion that the proterosuchids were mostly aquatic, predaceous reptiles living in ponds, lakes, and rivers, using swimming as their main form of locomotion, and preying upon other vertebrates. This conclusion is based on the similarity that they display in body form and proportions to modern crocodiles and in the characteristics of the skull and the dentition. Tatarinov (1961: 130) suggested that big forms like *Chasmatosaurus* fed upon fishes, and that the small forms like *Chasmatosuchus* might have been invertebrate eaters (how far invertebrates contributed to the diet of the proterosuchids is not clear). Moreover, the fact that proterosuchids have been found associated with unquestionable water dwellers, gives additional support to this conclusion. Hughes (1963: 221) affirms that in South Africa "bones of *Lystrosaurus* and *Chasmatosaurus* may be found side by side," and although Robinson (*fide* Hughes, 1963, same reference) cast doubts about the association of these two genera in the Panchet beds of India, this association, with the presence of labyrinthodonts as an additional element, has recently been reported by Satsangi (1964) in the Raniganj coal field. Moreover, Young (1936) reported the same fact in China. It must be recalled that *Lystrosaurus* is a dicynodont very specialized for an aquatic way of living, as indicated by the dorsally placed nostrils, the orbits projecting above the level of the roof of the skull, and the features of the carpus and tarsus. *Lystrosaurus* seems to have been an herbivorous animal not unlike the modern hippopotamus in habits, and its frequent association with the carnivorous *Chasmatosaurus* can be interpreted as an indication of food chain relationships between the two genera, the former playing the food role of a primary consumer fed upon by the latter, which played the role of a secondary consumer in the freshwater communities in which they lived. The pattern would, of course, be more complicated, since fishes and labyrinthodonts probably provided an additional food supply for the maintenance of the *Chasmatosaurus* populations, and since *Lystrosaurus* could have provided food for other pond predators, such as the big rhinesuchids that have been recorded in the *Lystrosaurus* Zone (see Watson, 1962). But the widespread occurrence of the *Lystrosaurus-Chasmatosaurus* association and the relative abundance of the former in the deposits are to be considered as good indications that the relationships of both these genera represented the dominant channel of energy flow in the food web of the communities to which they belonged.

Garjainia has been found in the deposits of the Russian Zone V, which is considered equivalent to the *Lystrosaurus* Zone. It is, in our belief, the first known erythrosuchid, and its position in the fossil record agrees with its possession of several intermediate features between proterosuchids and erythrosuchids (Charig and Reig, *in press*). The dentition is more carnivorous, and the skull shows modifications for a more efficient biting mechanism. The postcranial skeleton is unfortunately very little known. The skull characteristics of this genus are better developed in later erythrosuchids.

The way of life of more advanced erythrosuchids may be inferred from the skeletal morphology of the upper Lower Triassic genera (*Erythrosuchus, Shansisuchus, Vjushkovia*). Von Huene (1911: 20) pointed out that *Erythrosuchus* should be considered a mainly aquatic predator ("ein sich viel im Wasser aufhaltendes Raubtier"), maintaining that its enormous head can hardly be supposed to belong to an entirely terrestrial animal and that the same conclusion is supported by the structure of the remainder of the body ("Der plump Körper, der kräftige, aber relativ nicht lange Schwanz und namentlich der des grossen Schädels wegen aussergewöhnlich kurze Hals unterstützen die Annahme, das *Erythrosuchus* sich meist im Wasser aufhielt [Flüsse oder Tümpel]."). Tatarinov (1961: 131), on his part, although accepting that "the general proportions of its body, with a relatively huge head and short legs" indicate that erythrosuchids were tied to the water, seems inclined to believe that they were relatively more terrestrial than the proterosuchids, and stressed the carnivorous specializations of these animals, saying: "The main difference of the erythrosuchids with respect to the proterosuchids is related to the passage to an active carnivorous way of life" (Tatarinov, 1961: 130). We doubt that bulky and clumsy animals like *Erythrosuchus* or *Shansisuchus* should be considered very active animals, a point that has been emphasized by Young (1964: 146). It is more likely that they were inhabitants of swamp marshes, able to prey upon big, slow herbivorous vertebrates, inhabiting the same environments, which could be caught by a relatively slow and heavily built predator. In this connection, we may explore the question of what animals were the prey of the erythrosuchids.

Although evidence of certain association is not abundant, it is meaningful that the erythrosuchids can be considered animals that belonged to the same communities inhabited by the big, upper Lower Triassic dicynodonts of the families Kannemeyeriidae and Shansiodontidae (for a modern survey of these dicynodonts, see Cox, 1965). The most reliable association data are probably those coming from the deposits of the Ermaying Formation in China (Young, 1964; Sun, 1963). In several localities of this formation, bones of *Shansisuchus* and of *Erythrosuchus* were found, although not in actual association. Pearson (1924: 851) maintains that *Kannemeyeria* was a terrestrial animal that probably used its well-developed paws for digging or scraping in order to obtain its food, and she reported that Watson supposed that *Dicynodon* and *Kannemeyeria* lived on dry land. The origin of the giant dicynodonts of the Kannemeyeriidae is not well known but, as Cox (1965) has stated, the dicynodonts are hardly derivable from the aquatic and specialized lystrosaurids of the earlier level of the Lower Triassic. More probably they originated from some member of the vast array of Upper Permian dicynodontids, which are commonly considered herbivorous reptiles well adapted to living in terrestrial environments (see Watson, 1960: 201). The Middle Triassic representatives of the same group (kannemeyeriids and stahleckeriids) provide good evidence of association with terrestrial reptiles.

It can be argued that if the giant kannemeyeriids are derivable from the terrestrial herbivorous dicynodonts of the Upper Permian, the Lower Triassic Kannemeyeriids and shansiodontids should be also considered as upland dwellers. We believe, however, that this conclusion is not necessarily valid, and that the heavily-built and big-headed kannemeyeriids may be better thought of as inhabitants of shallow waters.

Moreover, there is no reason why, if the Upper Permian terrestrial dicynodontids should have been able to evolve into the fully aquatic lystrosaurids, they could not also have been the ancestors of semiaquatic marsh dwellers. Therefore, Pearson's interpretation of the habits of *Kannemeyeria* cannot be taken as conclusive.

If this reasoning is correct, proterosuchian evolution during Lower Triassic times can be interpreted as a shift from the aquatic and swimming predaceous way of life as represented by the proterosuchids, towards a shallow-water predaceous way of life, the shallow-water predators being adapted for slow walking in swamps. In the first case the main prey was the aquatic lystrosaurids, in the second case, the giant marsh-dwelling herbivorous kannemeyeriids.

In support of this conclusion, it is meaningful that the high point of the proterosuchids occurs in the *Lystrosaurus* Zone and equivalent levels of the lowermost Triassic, and that the erythrosuchids began to be abundant once *Lystrosaurus* itself became extinct. This seems to indicate that the shift in proterosuchian evolution from an aquatic towards a lowland marsh environment was necessitated by the extinction of the main source of food of the proterosuchid populations: the aquatic lystrosaurids. Once these became extinct, the originally aquatic proterosuchians were forced to look for their prey in the large herbivorous dicynodonts inhabiting the lowland marsh regions. This triggered the development of improvements for a walking locomotion and for large animal predation, both of which are characteristics of erythrosuchids. The sprawled condition of the legs is less efficient than the upright stance in a walking animal, but the latter is not completely necessary for slow animals hunting in shallow water environments for sluggish herbivores. This may explain how the erythrosuchids were successful animals in spite of the fact that they were sprawled and not very active predators and, at the same time, why they developed improvements for a walking locomotion as compared with the proterosuchids. In this sense, the changes in appendicular skeleton shown by the erythrosuchids, which do not reach a full degree of fitness for a terrestrial active locomotion, can be satisfactorily explained as an adaptive level suitable for a marsh dweller, and as a prospective adaptation (or a "preadaptation") for future terrestrial locomotion.

The fossil record also indicates that the proterosuchids did not become completely extinct after the *Lystrosaurus* zone and the extinction of the lystrosaurids, as one species of *Chasmatosaurus* has been reported in beds equivalent in age to the *Cynognathus* Zone (Young, 1964). Seemingly, the proterosuchids remained in their old environment as such, but were reduced in number and variety and played a secondary role in the aquatic communities. These aquatic proterosuchids from the upper part of the Lower Triassic, surviving after the detachment of the erythrosuchids, may well be the source of the other aquatic groups of archosaurs present in the record at later levels in the Triassic period.

The erythrosuchids seem to have become extinct by the end of the Lower Triassic. From the very beginning of the Middle Triassic other large predaceous archosaurs have been found in different parts of the world, representing a more terrestrial type; most of these belong to the family Rauisuchidae of the pseudosuchian thecodonts. At the same time, the evidence seems to indicate that at least some kannemeyeriids shifted towards a more terrestrial life in middle Triassic times, as their remains have been found associated with typical upland reptiles. The extinction of the erythrosuchids, however, and their replacement by more terrestrial thecodonts better adapted for upland and active locomotion could also be explained by a change in habitat of the animals representing the main source of food for carnivorous archosaurs. But in this case, the replacing group is not derivable from the replaced one, as the rauisuchids seem to have evolved from another group of Lower Triassic thecodonts, the pseudosuchians of the family Euparkeriidae. It will be of interest now, to review our knowledge of the proterosuchian descendants.

PROTEROSUCHIAN DESCENDANTS

It is here maintained that the Proterosuchia may be considered the stem archosaurian group, in which most of the subsequent evolution of archosaurs is rooted. The ways in which descent took place remain, however, rather obscure.

The taxa which seem most likely to have been derived directly from the proterosuchians are the Pseudosuchia and the Crocodilia. Saurischians and phytosaurs are also likely to be direct derivatives of the proterosuchians, but the evidence is far from being conclusive. The Ornithischia and the Pterodactyla are better thought of as descendants of the Pseudosuchia, but we are lacking the relevant data to advance any more secure opinions about them.

This theory does not agree with the classical view, which considers the pseudosuchian thecodonts as the ancestral group of later archosaurs, claiming that a tiny and bipedal pseudosuchian was the prototypical archosaur forebear from which the various dinosaurs, the pterodactyls, the crocodiles, and even the birds could have arisen. According to this view, bipedalism and small size, combined with fully terrestrial habits, are to be considered as primitive archosaur characteristics. We believe this widely-accepted hypothesis to be outdated and in direct contradiction to the evidence gathered in recent years. We shall develop our points of view in a brief analysis of some of the critical details.

Classification and evolutionary significance of the Euparkeriidae

The origin of the Pseudosuchia from the Proterosuchia is strongly supported by the existence of such an intermediate thecodont genus as *Euparkeria*, from the *Cynognathus* beds of the South African Karroo succession. *Euparkeria* has been recently revised by Ewer (1965) in an elegant work that added a great deal of information to our previous knowledge of it. Its evolutionary significance has been also discussed by this author and by Hughes (1963). It is profitable to make an additional analysis of the bearing of *Euparkeria* upon the classification and phylogeny of the thecodonts.

Ewer emphasized the intermediate nature of *Euparkeria*. This genus is remarkable for the fact that it shares proterosuchian and pseudosuchian character-states, which, of course, is the reason for the different familial allocations given to it by various authors. Both Ewer and Hughes are inclined to place *Euparkeria* within the Proterosuchia as a member of the family Erythrosuchidae. Previous authors generally placed *Euparkeria* within the Pseudosuchia (1) as a member of the family Ornithosuchidae (Tatarinov, 1964), (2) in a family of its own, Euparkeriidae (von Huene, 1920; Romer, 1956; von Huene, 1956), or, (3) rather oddly, in the family Sphenosuchidae (von Huene, 1962). Broom (1913), Heilman (1926), and Watson (1957) emphasized its central position among the Pseudosuchia, and thought of *Euparkeria* as a genus typifying the group from which the main lineages of the later archosaurs could have arisen.

Euparkeria shares with the Proterosuchia the following character-states of our list: 1, 2, 8, 9, 10, 12, 14, 15, 22, 23, 24, 26, and 28. This means that it has in common with the proterosuchians thirteen of the twenty-nine items of our analysis, and that it differs in the remaining sixteen. If we should apply a taxonomic criterion based on overall resemblance, *Euparkeria* would have to be placed in a taxon distinct from the Proterosuchia. Our approach is not, however, a phenetic one, and we are more attracted toward an evaluation of the character-states of this genus from an evolutionary point of view.

Eleven of the thirteen character-states shared by *Euparkeria* with the proterosuchians belong to our *AS* class. They are primitive archosaurian (and pre-archosaurian) features that evolved slowly during the first states of the archosaurian evolution. On the other hand, as these character-states are present in all the proterosuchians, they do not afford clues by which to investigate the affinities of *Euparkeria* within the Proterosuchia. More significant is the agreement of this genus with the proterosuchians in two of the three *SS* character-states: the presence of palatal teeth and the presence of intercentra.

Palatal teeth are known to be possessed by the proterosuchids, but not by the erythrosuchids. Intercentra are present in *Euparkeria* through all the length of the presacral vertebrae, just as in *Chasmatosaurus*. *Erythrosuchus* is the only erythrosuchid having intercentra, and they are present only in the cervical region of the column. These facts could be interpreted as an indication that the erythrosuchids were not the ancestors of the euparkeriids, and that the latter arose somewhere within the proterosuchids as a separate lineage. However, the erythrosuchids show features in the dentition, the skull, and the appendicular skeleton, that relate them more closely to the euparkeriids than to any of the proterosuchids. If one were to infer relationships by overall resemblance, it would be safe to conclude that the euparkeriids are more closely related to the erythrosuchids than to the proterosuchids. Palatal teeth and intercentra are, in spite of that, a true challenge to erythrosuchid derivation. An additional hint in the same direction is afforded by the presumed way of life of *Euparkeria.* As Ewer pointed out, this genus was a predator upon tiny vertebrates and invertebrates living in upland regions, and, as such, was capable of rapid locomotion in a terrestrial environment. This kind of animal is hardly derivable from such bulky and sluggish marsh dwellers as the contemporary erythrosuchids seem to have been. These contradictions can be overcome if we visualize the origin of the euparkeriids as an event that took place during the transitional phase of the proterosuchid-erythrosuchid descent. At this stage, the transitional forms should have retained some of the primitive proterosuchid character-states, and they should also have acquired some of the morphological and ecological traits of the erythrosuchids. These proterosuchians would have lived in a transitional ecological zone where selective pressures would have rewarded any acquisition for a better adaptation as predators of great size dwelling in lowland marshes, and also any change improving upland fast locomotion, air-wave hearing, biting efficiency, and water economy, all of which are necessary acquisitions for active terrestrial predators. Directional selection would have created, in the first case, the typical erythrosuchids; in the second case, the euparkeriids.

It is meaningful in this connection that the euparkeriids differ from both erythrosuchids and proterosuchids precisely in those characters that can be correlated with functions linked with upland rapid locomotion, air-wave hearing, masticatory efficiency, and, presumably, water economy. *Euparkeria* shows changes to a different state in, among others, items 16, 17, 18, 19, 20, 21, and 25 of our list of proterosuchian character-states. In all those cases, the changed state of the character in *Euparkeria* was evidently linked with improvements for a more efficient terrestrial locomotion: upright stance; hind limbs longer than the fore limbs to a greater degree than in the proterosuchians; femur without intertrochanteric fossa or internal trochanter; humerus with less expanded ends; tarsus with incipient specializations in the ankle joint, thus anticipating developments in the later pseudosuchians; a longer pubis and ischium representing a more advanced type of triradiate pelvis. At the same time, the development of a fully evolved otic notch shown by *Euparkeria,* distinct from proterosuchian character-state 4 and correlated with changes in the state of character-states 5 and 6, is to be interpreted as an improvement for better air-wave hearing, the otic notch being obviously an improved device in this direction, as it gives room for, and enhances the function of, the tympanic membrane.

Concerning the changes in the biting mechanism, Watson (1957) and Ewer (1965) demonstrated how far the shifting forward of the suspensorium, moving the quadrate towards a more vertical position, is a necessary development toward increasing the height of the temporal region and correlatively toward lengthening the fibers of the temporal musculature for a more efficient biting action. This development is fully attained in *Euparkeria,* and in this genus it is correlated with an enlargement of the upper temporal opening, which provides additional area for the insertion of the *pseudotemporalis* muscle, and with the development of a dentition more specialized for a predaceous way of life.

Ewer has convincingly argued against

the interpretation of the antorbital fenestra as an area of insertion of the *pterygoideus D.* muscle maintained by Dollo, Gregory and Adams, and Walker. She stresses the possibility that this fenestra might have housed a large salt gland, as suggested by Broom (1913). It is now well known that not only several marine vertebrates (Schmidt-Nielsen, 1958) but also desert lizards such as *Ctenosaura* and *Sauromalus* (see Templeton, 1964, 1966) have nasal salt glands that play an important role in removing chloride salts from the body, with a small loss of water, thus acting as an extrarenal mechanism for salt excretion and water economy. The known cases of the presence of nasal salt glands of this sort in living vertebrates do not show this gland housed in an antorbital fenestra, but we do not believe that this fact need be a serious challenge to the interpretation of Broom and Ewer. Though admittedly highly speculative, the following reasoning is presented as a possible explanation of the known facts concerning this problem.

As the mammals are urea-secreting animals derived from the pelycosaurs through the therapsids, it can be assumed that the pelycosaurian ancestors of the archosaurs were also ureotelic animals, and that uricotelism developed only later in their archosaurian descendants (the birds are typically uric acid-secreting animals). Uricotelism being related with water economy in animals living in dry conditions, the lack of this metabolic device in the increasingly upland dwelling archosaurs may have been balanced by the development of an extrarenal salt-secreting device. If the antorbital fenestra is actually the site for a salt gland, this may explain the characteristic development of such an opening in all the archosaurs. In this connection, *Euparkeria* clearly shows an improvement beyond the proterosuchian level, as it has a larger antorbital fenestra lodged in a basin-like depression, which indicates a bigger size, and hence, an intensification of the function of the salt gland. This intensification of function of an extrarenal salt-secreting organ can be thought of as an improvement of the adaptation to upland, dry environments, in ureotelic animals coming from a freshwater environment in which economy of water was not necessary. The presence of a small antorbital fenestra in *Proterochampsa* and later crocodiles agrees with this argument; the presence of a large antorbital fenestra in phytosaurs, however, is not consistent with it.

For all these reasons, it seems evident that *Euparkeria* has departed from the proterosuchian level of evolution in significant respects. As most of its innovations are also well developed in the pseudosuchian thecodonts, it is reasonable to think of it as a member of the group representing the early shift of the thecodonts towards the upland life to fulfill the roles of terrestrial carnivorous reptiles, a shift that triggered the radiation of the Middle and Upper Triassic pseudosuchians. In this sense, the new character-states shown by *Euparkeria* in locomotion, biting mechanism, hearing, and water economy are to be interpreted as key innovations opening up new evolutionary possibilities and enhancing the emergence of a new major taxon, which in this case is the suborder Pseudosuchia of the Thecodontia.

In spite of the fact that *Euparkeria* (with *Browniella* as a junior synonym) is the only Lower Triassic slightly-built pseudosuchian known from skeletal remains, the available evidence shows that thecodonts that had already attained the same level of evolution were widespread in upper Lower Triassic and lower Middle Triassic times. This evidence comes mainly from ichnological data, which indicates that quadrupedal, lightly built, and small-sized pseudosuchians flourished by that time in North America (Peabody, 1948). As contended by this and other authors, it is quite probable that the large manus footprints of the chirotheriids of small size were actually made by euparkeriid thecodonts. At the same time, it is also possible that some dubious skeletal remains of the same general age could in the future be demonstrated as belonging to the same family. *Wangisuchus*, a genus based on fragmentary remains of various individuals, has been referred by Young (1964) to this family. The basis for this assignment is not clear, however.

The known skeletal structure of *Euparkeria* makes it clear that this genus had not attained certain of the specializations that are full-fledged in the Middle and Upper Triassic pseudosuchians that are probably euparkeriid derivatives. This fact supports the splitting off of *Euparkeria* into a family of its own, distinct from the remaining families of the Pseudosuchia. As far as the relationships of the euparkeriids with the other pseudosuchians are concerned, one could say that with respect to the remaining pseudosuchians, the euparkeriids hold the same relationship that the Proterosuchians hold with respect to the whole of the non-proterosuchian archosaurs.

Relationships with the Pseudosuchia

The remaining Middle and Upper Triassic thecodonts are far from affording a clear-cut picture of their evolutionary relationships and classification. It has been said that the Pseudosuchia are a sort of waste-basket, a statement that seems to cast serious doubts about the naturalness of the group. The Pseudosuchia seem to be, however, a natural group, but it is evident that the whole taxon is in need of a thorough revision. Some recent papers by Krebs (1963, 1965), Reig (1961), Sill (1967), Walker (1961, 1964, 1966), and others have already contributed to a great extent to clearing up the status of parts of this taxon.

It is now agreed that the Elachistosuchidae must be ruled out of the Pseudosuchia, as *Elachistosuchus* has been demonstrated by Walker (1966) to belong to the rhynchocephalians. At the same time, Sill (1967, see also below) suggested that the crocodiloid thecodonts usually placed in the superfamily Sphenosuchoidea of the Pseudosuchia, are better considered as belonging to the protosuchian crocodiles. After these deletions, the main subordinate taxa of the Pseudosuchia are the Lower (and Middle?) Triassic Euparkeriidae, the Middle Triassic Rauisuchidae, the Middle and Upper Triassic Stagonolepididae (see below) and the probably related Upper Triassic Stegomosuchidae,[1] the Upper Triassic Ornithosuchidae, and the Upper Triassic Scleromochlidae. It will now be useful here to assess the main conclusions that can be drawn from present knowledge of the pseudosuchians (Fig. 10).

All pseudosuchian families share the following characters: possession of an otic notch; suspensorium shifted forward; V-shaped contour of the posterior border of the lower temporal opening; large antorbital fenestra lying in an extended basin-like depression (with the exception of *Rhadinosuchus* and *Clarenceia*, see later); fairly large nares close to the antorbital fenestra (same exceptions); pterygoids joined at the midline; palatal teeth absent (with the exception of *Euparkeria*); marginal teeth subheterodont and thecodont; intercentra absent (with the exception of *Euparkeria*); advanced quadrupedal or bipedal gait; posterior limbs somewhat longer than the front ones; propodials vertical in position; pes "crocodiloid," with astragalocrural—calcaneum-tarsal ankle joint (incipiently so in *Euparkeria*); calcaneum with a tuberosity; long pubis and ischium; well-developed dermal armor (except in *Scleromochlus*, surely a secondary loss). It seems clear that the above intension of the concept of Pseudosuchia makes this taxon a well-defined one with respect to the Proterosuchia.

The pseudosuchian character-states evolved seemingly as an adaptation to

[1] Walker (1968), however, has recently maintained that the Stegomosuchidae are crocodiles; see Addendum.

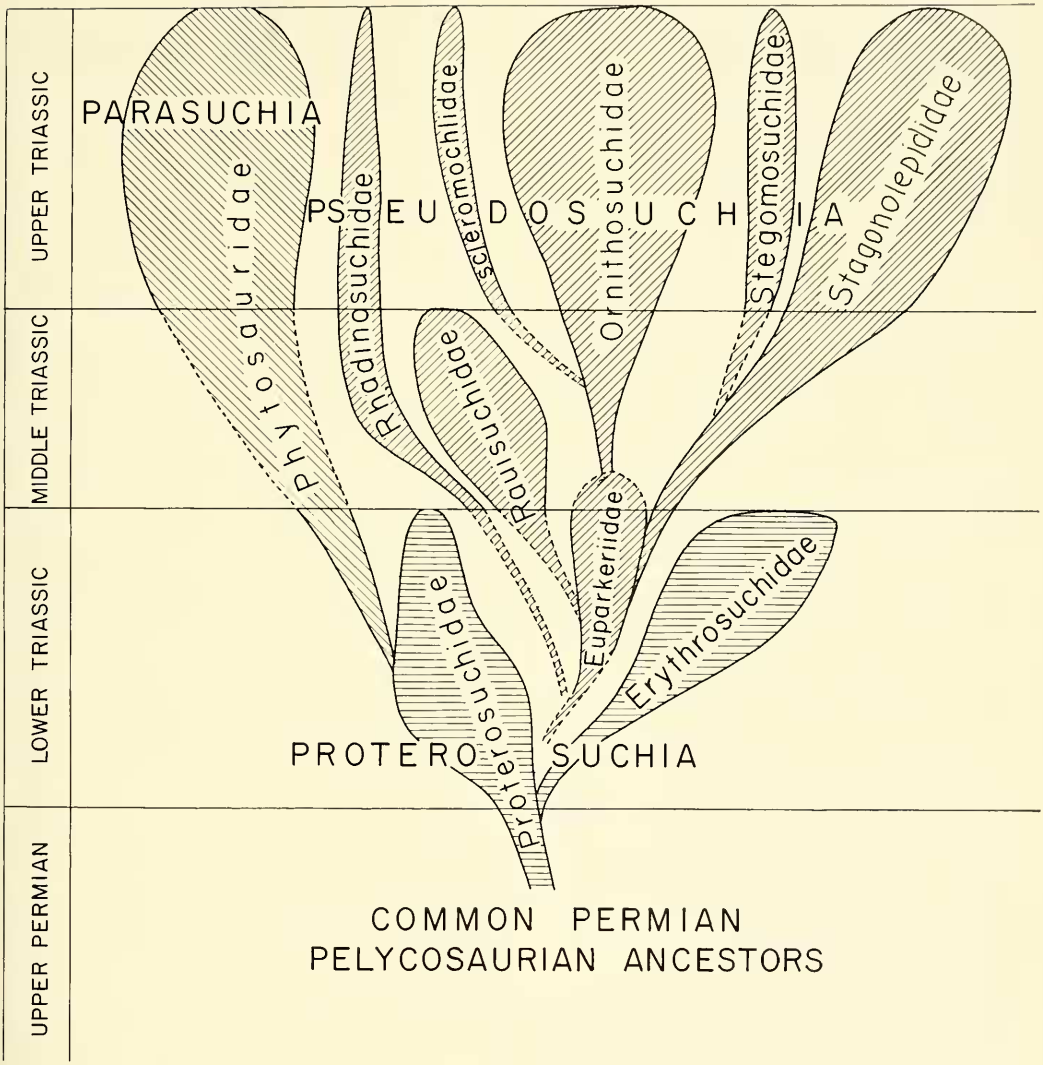

Figure 10. Phylogenetic diagram of the suggested relationships among the various families of the Pseudosuchia and the other thecodonts.

terrestrial life, and for the most part they were already established in the euparkeriids. The rauisuchids probably evolved as a branch divergent from the euparkeriid stock in the early Middle Triassic or uppermost Lower Triassic. Their first well-documented representative is *Ticinosuchus* from the Anisian of Europe (Krebs, 1965). Young (1964) referred to the same family the upper Lower Triassic Chinese genus *Fenhosuchus* because of some similarities in vertebral morphology, shape of the scutes, and other dubious characters. This genus is known from fragmentary bones of various individuals, and its status is far from clear. Nevertheless, the presence of rauisuchids in the Lower Triassic is suggested again by the ichnological evidence, as large-sized quadrupedal chirotheriids of probable rauisuchid relationships have been found in beds of Scythian age in Germany, North America, and South America (see Peabody, 1948, 1955; Krebs, 1965). Apart from those mentioned above, rauisuchids are known in Middle Triassic (lower Ladinian?) beds of Africa (*Stagonosuchus* of the Manda beds of Tanganyika) and Brazil (*Rauisuchus, Prestosuchus* from the Santa Maria beds of Rio Grande do Sul) and in the upper Middle Triassic (upper Ladinian?) of Argentina (*Saurosuchus* from the Ischigualasto beds of San Juan Province). The rauisuchids seem to have been reptiles well adapted for terrestrial life, and they reached a great size. They were surely huge predators more active and efficient than the erythrosuchids, but they remained quadrupedal like the latter, perhaps because of the attainment of a bulky body and a great weight before the full acquisition of the necessary limb modifications for bipedal stance and locomotion. Advance beyond the euparkeriid level is shown, however, in the full development of a crurotarsal crocodiloid ankle joint, the great elongation of the ventral pelvic bones, the loss of palatal teeth, and the pterygoid union at the midline (as shown in *Saurosuchus*, unpublished personal data), the loss of postparietal and postfrontal bones, and large size. The rauisuchids became extinct at the end of the Middle Triassic, apparently without giving rise to any other group, and perhaps because of the competition of the carnosaurian saurischians. It is also probably meaningful that their spread and diversification from the beginning of the Middle Triassic can be correlated with the extinction of the erythrosuchids at the end of the Lower Triassic.

Another well-defined family of pseudosuchians is the Stagonolepididae.[1] Reig (1961), Walker (1961), and Krebs (1965) have demonstrated that the stagonolepidids are not as closely related to the rauisuchids as is maintained by some authors. Nevertheless, Reig's contention that the two families must be placed in different suborders now appears too exaggerated a view, as it is quite possible that the two families originated in the euparkeriids. The stagonolepidids are, of course, a very clear-cut group, as their specializations in bony armor and in skull and dentition are unique among the thecodonts. That the family was fully established in upper Middle Triassic times is demonstrated by *Aëtosauroides* from the Ischigualasto beds of Argentina (Casamiquela, 1961). They may have separated from the euparkeriid stock in early Middle Triassic times, evolving as an independent lineage that played its own distinct ecological role. *Aëtosaurus* from the German Keuper, *Stagonolepis* from the Elgin Sandstones of Scotland, and *Typothorax, Desmatosuchus, Acompsosaurus,* and *Stegomus* from the Upper Triassic of North America demonstrate that the family was rather widespread in Keuper times.

Though the way of life of the stagonolepidids is still a matter of controversy, it is evident at least that the members of this family were completely terrestrial pseudosuchians and that they are to be regarded as the first archosaurs that were not predators. Walker has supposed that they were mostly herbivorous, while Sawin (1947) maintained that they were scavengers. It is interesting to realize that the stagonolepidids share some general resemblance with the dasypodids, both in the possession of dermal armor and in the general shape of the skull and dentition, a point that would bolster the scavenger hypothesis, but which does not necessarily exclude the assumption of a rather com-

[1] I agree with Walker in including in one family all the genera of thecodonts currently referred to the families "Stagonolepidae," Aëtosauridae, and Desmatosuchidae. The correct familial name for this assemblage is Stagonolepididae Lydekker, July 1887, a name that antedates Aëtosauridae Baur, September 1887. Von Huene's "Stagonolepidae" (1908), so frequently encountered in the literature, is etymologically incorrect.

posite and variable diet, with vegetables and arthropods as usual components.

Stegomosuchus and *Dyoplax*, from the Upper Triassic of North America and Europe, respectively, are rather poorly known genera showing several resemblances to the stagonolepidids in armor development and other features. They may be closely related to the aëtosaurids in origin, but if they are really related to each other, they should be placed in a separate family Stegomosuchidae.

The taxonomic status and the relationships of the remaining pseudosuchians are less clear. Most of the non-rauisuchid and non-stagonolepidid genera are commonly grouped in the family Ornithosuchidae, which is supposed to include small or medium-sized, bipedal predators, of which *Ornithosuchus* would be a typical example. However, this genus has been recently demonstrated by Walker (1964) to include fairly large animals, and the large *Dasygnathus* from the same Elgin Sandstones that yielded the original remains of *Ornithosuchus* is placed by him in its synonymy. Walker also arrives at the odd conclusion that *Ornithosuchus* is neither a pseudosuchian nor any other kind of thecodont, but that it is better placed within the order Saurischia. This latter view is rather difficult to agree with, and the present author has not found in Walker's new data and appraisals sufficient supporting reasons for such an astounding upheaval of the current arrangement.

It is true that *Ornithosuchus* looks like the carnosaurian dinosaurs in several respects, but the instances of resemblance are better ascribed either to the sharing of general archosaurian features or to the fact that *Ornithosuchus* and the carnosaurs attained, in parallel, specializations for bipedal locomotion and a predaceous way of life. On the other hand, Walker did not attempt to demonstrate that this genus is not a pseudosuchian, his argument being directed to support of the view that it is a carnosaur. We think that important reasons are at hand for keeping *Ornithosuchus* in the Pseudosuchia. One of them is the possession of the double line of paramedial scutes, a character-state shared by the euparkeriids, the rauisuchids, and some genera referred to the ornithosuchids, and which is to be considered as an original pseudosuchian feature from which evolved the armor of such heavily armored forms as the stagonolepidids. No certain evidence of dermal armor is known for the Carnosauria; the alleged carnosaurian scutes from the Upper Cretaceous of India are better referred to ornithischian dinosaurs (see Walker, 1964: 117–119). Another important point is that *Ornithosuchus* has, almost surely, a typical pseudosuchian ankle joint. The carnosaurs, like all the saurischians, have a completely different type of ankle joint, which is hardly derivable from such a specialized structure as the pseudosuchian-crocodiloid tarsus (see below). In other respects, *Ornithosuchus* agrees perfectly with the pseudosuchian character-states. It seems rather bizarre to claim that it is a carnosaur when it is not really separable from the thecodonts. Walker admits that "it might ultimately prove necessary to retain *Ornithosuchus* in the Pseudosuchia" (1964: 110), a statement that does not seem to fit very well with his previous affirmation that only the coelurosaurs and the carnosaurs "need be seriously considered in a discussion of the affinities of *Ornithosuchus*" (1964: 105).

Walker also maintains that *Ornithosuchus* lies morphologically close to the boundary between the pseudosuchians and the carnosaurs, and that phylogenetic relationships are more clearly expressed by placing it with the carnivorous dinosaurs. In fact, this seems not to be the case, as typical carnosaurian and other saurischian dinosaurs have been found in beds definitely earlier than the Elgin Triassic (see Reig, 1963a; Charig, Attridge and Crompton, 1965; Ellenberger and Ginsburg, 1966). These finds clearly prove that by the Middle Triassic several lineages of saurischians were already differentiated, and this suggests that the origin of the group is to be sought as early as the Lower Triassic. The Upper Triassic *Ornithosuchus* cannot be considered as intermediate for temporal reasons, and there are no cogent grounds for placing it anywhere but in the Pseudosuchia. It is more reasonable to believe that within that suborder of thecodonts, one family attained bipedalism and other carnivorous specializations, paralleling some lineages of contemporary dinosaurs with which it entered in competition. If we retain the family Ornithosuchidae and include in it not only the large-sized *Ornithosuchus,* but also the tiny genera *Saltoposuchus* and *Hesperosuchus,* we may agree that the ornithosuchids paralleled both the coelurosaurs and the carnosaurs in general appearance and ecological roles.

The curious *Scleromochlus* may be considered as an arboreal derivative of the Ornithosuchidae, distinct enough to warrant familial separation. There remain, however, other pseudosuchian genera that are less clear as to family allocation. *Erpetosuchus,* from the Upper Triassic of the Elgin Sandstones, has been commonly classified with the ornithosuchids, but other opinions have resulted in the erection of a family of its own for this genus. Walker (1961) places *Erpetosuchus, Dyoplax,* and probably *Stegomosuchus* in the family Erpetosuchidae, an arrangement that seems unnatural to the present author. The place of this genus is better considered as unsettled until a modern revision is undertaken.

As far as *Cerritosaurus* (Price, 1946) from the Santa Maria Middle Triassic of Brazil is concerned, it is almost surely, as suggested by Hoffstetter (1955), a junior synonym of *Rhadinosuchus* von Huene. This genus is very peculiar in the small size of the antorbital fenestra, the size and the position of the external nares, the obliteration of the postemporal fenestra, and the straight posterior border of the lower temporal opening. These features make this genus hardly derivable from the euparkeriids, and some of them are actually proterosuchian, non-pseudosuchian character-states. Nevertheless, it has acquired pseudosuchian status in such characters as the absence of postfrontal and postparietal bones, the presence of an otic notch, and the thecodont and subheterodont dentition. If *Rhadinosuchus* is actually a pseudosuchian, it could represent a family of its own, Rhadinosuchidae, as proposed by Hoffstetter (1955) and accepted by Kuhn (1961). This family might have originated independently within the proterosuchians, reaching the pseudosuchian level in its own way. Another poorly known genus from the Upper Triassic of South Africa, *Clarenceia* (see Brink, 1959), agrees with *Rhadinosuchus* in the structure of the antorbital fenestra and the form of the maxilla, and might belong to the same family (Romer, 1966b, makes this genus a dubious member of the Ornithosuchidae, a position that seems to lack relevant foundations). If our interpretation of *Rhadinosuchus* is right, the implication is that either we accept the Pseudosuchia as a polyphyletic assemblage, or we must allow for the inconvenience of erecting a new suborder to accommodate *Rhadinosuchus* and allies. Our knowledge of these forms is, however, too imperfect to support any formal proposal of changes in the system of the Thecodontia.

The origin of the crocodilia

The crocodiles have been classically considered as descendants of the Pseudosuchia. Within the latter, the Sphenosuchidae from the Upper Triassic of South Africa were considered to be the ancestral group. Primitive crocodilian archosaurs such as *Notochampsa* and *Pedeticosaurus* (from the Cave Sandstone beds of the Stormberg Series of South Africa), *Erythrochampsa* (from the underlying Red Beds, which also yielded *Sphenosuchus*), and *Protosuchus* (from the later Triassic or earliest Jurassic of Arizona), commonly grouped in the crocodilian suborder Protosuchia, have been regarded as transitional between the ancestral sphenosuchids and the later typical crocodiles (Mesosuchia, Sebecosuchia, Eusuchia). According to this conception, the assumption is made that the crocodiles evolved from primitively bipedal pseudosuchians, and that they returned to a quadrupedal gait as an adaptation to the amphibious way of life (for broader information on these ideas on crocodilian origins, see Haughton, 1924; von Huene, 1925; Colbert and Mook, 1951; Kälin, 1955).

Recently, Sill (1967) has made a thorough reappraisal of the question, on the basis of the bearing of *Proterochampsa* upon crocodilian origins. *Proterochampsa* (Reig, 1959) (Fig. 11) is an obvious crocodile from the late Middle Triassic Ischigualasto beds of Argentina, showing a remarkable combination of primitive, transitional, and advanced character-states. It is the earliest crocodile so far known, and it is definitely earlier than the sphenosuchids reported to be the pseudosuchian ancestors of the crocodiles.

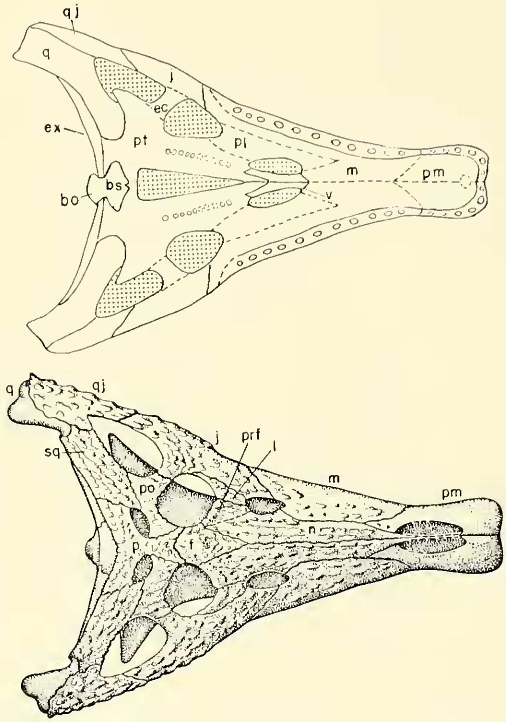

Figure 11. Ventral and dorsal views of the skull of *Proterochampsa barrionuevoi* Reig. (After Sill.)

The crocodilian nature of *Proterochampsa* is evident from the morphology of the dorsal surface of the skull, the presence of a rudimentary secondary palate built up by the premaxilla and the maxilla, the sculptured bones of the roof of the skull, and the structure of the vertebral apophyses. Besides this, it is noteworthy that the anterior foot shows the typical carpal specializations of modern crocodiles: elongated radiale and ulnare carpal bones. This is demonstrated by a nearly complete anterior leg found in association with the remains of a coelurosaurian dinosaur in the Ischigualasto beds (Reig, 1963a).[1] The femur and the humerus, known to the author through undescribed specimens associated with skull remains, are also typically crocodiloid. Unfortunately, bones of the girdles have not been found so far. As pointed out by Sill (1967), it is meaningful that *Proterochampsa* is in several respects more crocodilian than the later genus *Protosuchus*.[2]

The implication of the discovery of *Proterochampsa* is that the sphenosuchids can no longer be considered as the thecodont ancestors of the crocodilians, nor can *Protosuchus* and its allies be thought of as a transitional group between the pseudosuchians and the later full-fledged crocodiles. Sill has made a suborder Archaeosuchia to group together both the Middle Triassic monotypic family Proterochampsidae and the Upper Triassic Notochampsidae (including *Notochampsa* and

[1] See, however, the Addendum.

[2] For another view on the place of *Proterochampsa* and other early crocodiles, see Walker (1968) and the Addendum.

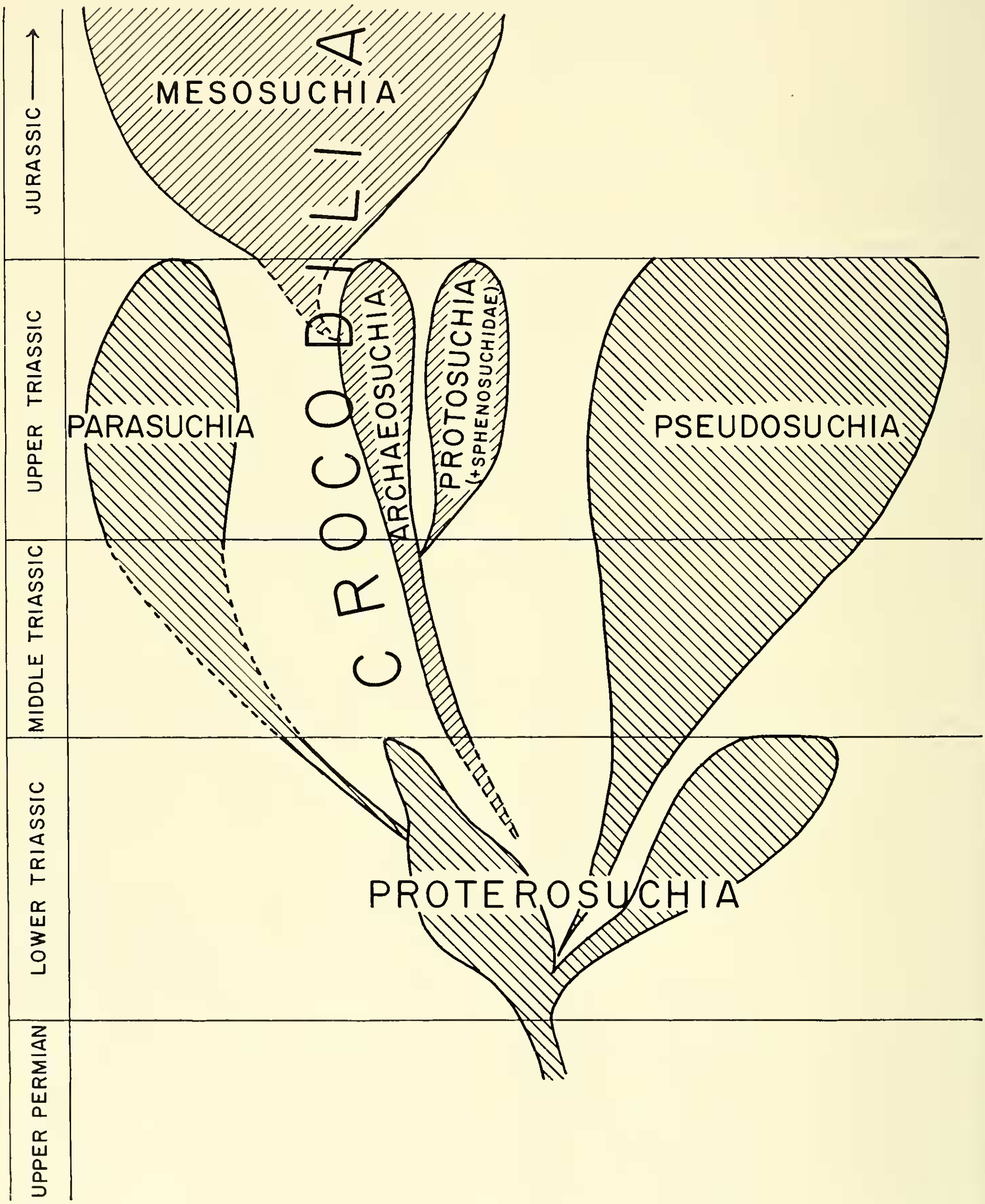

Figure 12. Phylogenetic diagram of the probable origin of crocodiles and the relationships among the various crocodilian and thecodontian suborders.

Erythochampsa). He believes that this suborder is the ancestral group of the Mesozoic and modern crocodiles of the suborders Mesosuchia, Sebecosuchia, and Eusuchia (Fig. 12). *Protosuchus*, on the other hand, would represent a suborder, the Protosuchia of Mook (1934) and later authors, that has departed from the main direction of crocodilian evolution by adaptating to a more terrestrial way of life. As Sill has proposed and Romer (1966b) has accepted, the Sphenosuchidae and such dubious genera as *Pedeticosaurus* and *Platyognathus* are better grouped within the Protosuchia, since they agree with *Protosuchus* in the sharing of an early crocodilian heritage with adaptations for a more terrestrial life. Referring to these animals, Sill uses an expression coined by Kermack: they are "crocodiles trying to be dinosaurs." This meaningful expression describes perfectly the evolutionary trend in these atypical crocodiles for a dinosaur-like (i.e. terrestrial and predaceous) way of life.

Sill advances two alternative hypotheses for crocodilian origins: either they originated from a non-pseudosuchian group of aquatic thecodonts, or they descended from a primitive group of terrestrial thecodonts, possibly early pseudosuchians. As we have already seen, the euparkeriids make perfect early pseudosuchians in their organization. *Proterochampsa* is, however, hardly derivable from euparkeriid ancestors for the following reasons: (1) it has not developed the typical pseudosuchian otic-notch; (2) it has a primitive and small antorbital fenestra; (3) it has not acquired the pseudosuchian V-shaped contour of the posterior border of the lower temporal opening; and (4) it has the suspensorium placed backwards. These are actually proterosuchian character-states, and *Proterochampsa* is also proterosuchian in the possession of palatal teeth and in the shape and proportional size of the temporal openings.

This gives support to the first of Sill's two alternative hypotheses, suggesting that the Archaeosuchia (and through them, all the crocodiles) might have been derived from the aquatic proterosuchians of the Lower Triassic. It should be remembered that after the separation of the erythrosuchids, proterosuchids were represented in beds equivalent to the *Cynognathus* Zone. These late aquatic proterosuchians could have been the ancestors of other lines of aquatic archosaurs.

Nevertheless, one important point remains unexplained if we accept Sill's first alternative. Crocodiles and pseudosuchians (and probably phytosaurs) share the possession of a peculiar type of ankle joint, the so-called "crocodiloid" tarsus, in which the functional joint lies between the astragalus and calcaneum, these being articulated by means of a ball-and-socket type of joint. As we have already seen, this kind of tarsus is not a primitive archosaur characteristic, as both proterosuchids and erythrosuchids show quite another, more primitive, type of ankle. Walker's belief (1964: 110) that the crocodilian ankle-joint "may after all represent a basic archosaurian pattern," is therefore lacking a serious basis. Krebs (1963) has pointed out that the resemblance between pseudosuchians and crocodiles in tarsal structure is so great that it is difficult to think that such a tarsus arose independently in both groups by convergent evolution. It must be realized that the hypothetical common ancestral group for both crocodiles and pseudosuchians, required by tarsal structure, could not be identical with the euparkeriids, as *Euparkeria* has not reached full development of such a type of ankle joint. This means either that the supposed common ancestor should be sought at a post-euparkeriid level of thecodont evolution or that it must be accepted that the character-state under discussion developed independently in pseudosuchians and crocodilians. The first possibility seems to be ruled out, as the characteristics of the archaeosuchians do not permit thinking of a common ancestry even at the level of the euparkeriids. It would be very useful to have information about the structure of the ankle in *Proterochampsa*, which, unfortunately, is not available thus far.

In our present state of knowledge it seems best to adhere to the hypothesis of the proterosuchian origin of the crocodilians, and to accept the idea of the convergent evolution of the type of ankle found in both crocodiles and pseudosuchians. It must be admitted, however, that the evidence is still too incomplete to permit a fully satisfactory explanation of crocodilian origins, and that a better knowledge of Lower and Middle Triassic thecodonts may make it necessary in the future to introduce changes in the present explanation. At this point, it is interesting to recall the Rhadinosuchidae, a Middle Triassic group of scarcely known thecodonts that seem to have reached the pseudosuchian level from an ancestry distinct from the euparkeriids. It will not be surprising if a better understanding of these forms throws light on questions of the kind raised here.

Saurischian ancestry

The ancestry of the saurischian dinosaurs is also commonly explained by hypotheses that advocate that the pseudosuchian thecodonts were the ancestral group. Until recently, the first unquestionable saurischians were known only from beds of Upper Triassic age; indeed the presence of dinosaurs has been considered conclusive evidence for dating Triassic strata of dubious age as Upper Triassic. Coelurosaurs, carnosaurs, and prosauropods were known from the Upper Triassic, and all three groups were supposed to derive from a single source in the Upper Triassic, namely allegedly tiny, bipedal, carnivorous pseudosuchians similar to the ornithosuchids. According to this conception, the quadrupedalism of the sauropods was secondary and derived from a primitive bipedal condition.

Our intent here is not to essay an exhaustive look at the rather confusing situation of the Triassic saurischians. This task has been partially carried out by Charig, Attridge, and Crompton (1965), Colbert (1964), and Walker (1964), and work by these and other authors will surely contribute to a better understanding of the group. We need, however, to present a very general survey of the present status of knowledge about Triassic saurischians in order to frame the question of saurischian origins as coherently as possible in terms of its factual foundations, and thus to check to what extent the existing stereotyped opinions on saurischian origins are supported by the available evidence.

The Upper Triassic faunas of the world differ sharply from the Middle and Lower Triassic ones in the abundance and variety of their dinosaurs. Romer (1966a) recently made it clear that in spite of semantic discussions on the rather conventional question of the boundary between Middle and Upper Triassic, the faunas currently referred to the Middle Triassic are distinct from those usually referred to the Upper Triassic by the fact that their dominant groups are different. Gomphodonts and rhynchosaurs are dominant in the B assemblages (Middle Triassic); dinosaurs are the dominant group in the C faunas (Upper Triassic). The same synecological criterion has been used in Reig's (1963a) discussion of the age of the Ischigualasto beds, a criterion that seems not to have been sufficiently grasped by Bonaparte (1966) in his recent discussion of the Argentinian vertebrate-bearing Triassic. These Upper Triassic faunas are known in the European Keuper, the Red Beds and Cave Sandstones of South Africa, the Forest Sandstones of Southern Rhodesia, the Dockum and Chinle of North America, and the Lufeng Series of China. The Los Colorados beds and the El Tranquilo Formation of Argentina, the faunas of which are now being studied by Bonaparte and Casamiquela, probably belong to the same group.

Faunas of the B type are known in South America (Santa Maria, Ischigualasto, Chañares), Africa (Manda beds, Molteno beds, Ntaware Formation), and India (Maleri beds). Some faunas, such as those from the Elgin Sandstones (Scotland) and Maphutseng (Basutoland), seem to be transitional between the B and C assemblages.

The saurischians of the late Triassic faunas belong to three different infraorders, which are clearly recognizable at the time of their first appearance in the Lower Triassic, namely the Coelurosauria, the Sauropoda, and the Palaeopoda (I use here Colbert's [1964] new name instead of Prosauropoda, as this last concept is confusing both in intension and in extension). The coelurosaurians are represented in the Upper Triassic by the family Podokesauridae, Hallopidae, and Segisauridae (the second not surely distinct from the first). They were slightly-built upland predators, distinguished from other contemporaneous dinosaurs by the "dolichoiliac" pelvis (Colbert, 1964), advanced bipedal gait, birdlike feet, calcaneum usually with a tuber, long neck, relatively elongated skull. It is now clear that the true Carnosauria of the Jurassic and Cretaceous are an offshoot of the Coelurosauria, with which they share the same type of pelvis, the birdlike feet, and many other features. Both infraorders are therefore grouped in the suborder Theropoda of Marsh, giving to this taxon-concept a narrower extension than that in the current conservative classification.

The Sauropoda are represented from the very beginning of the Upper Triassic by the Melanorosauridae. This family is usually placed within the "Prosauropoda" (= Palaeopoda). Recent work by Ellenberger and Ginsburg (1966) demonstrates that they are quadrupedal and very close to the true sauropods. These authors and Attridge (1963) suggested that the melanorosaurids should be considered true sauropods, a suggestion that seems very reasonable to me. Though disregarding the melanorosaurids as direct ancestors of the sauropods, Charig *et al.* have convincingly demonstrated that "the line of evolution which led from the pseudosuchians towards the sauropods was entirely quadrupedal; thus the sauropods were not, as commonly supposed, quadrupedal reversions from bipedal forebears.

"The various families of prosauropods were offshoots from this main, quadrupedal sauropodomorph line, representing adaptations to different habitats which differed especially in their degree of bipedality; none survived the Trias" (1965: 205). From the new evidence provided by Ellenberger and Ginsburg (1966), one arrives at the conviction that the melanorosaurids should belong to this "main, quadrupedal sauropodomorph line" which, from its very beginning, was part of the evolution of the true sauropods. Melanorosaurids are known from the Middle-Upper Triassic boundary, as represented by the remains referred to *Euskelosaurus* by Ellenberger and Ginsburg (1966), which come from the "Passage beds" of Basutoland (the "Maphutseng dinosaur" of Charig *et al.*, 1965); a hind leg from the same beds described by Crompton and Wapenaar (in press) (reported by Charig *et al.* as the "Blikana dinosaur"); and the "Soebeng trackways," footprints of a big quadrupedal dinosaur, mentioned by the above authors and by Ellenberger and Ginsburg (1966). Besides these early finds, melanorosaurids are relatively abundant in the Red Beds of South Africa. The Melanorosauridae are likely to have been herbivores and swamp-dwellers; the possibility that the family would include carnivorous forms has been suggested by Charig *et al.* (1965), but there are good reasons to doubt this. The evidence supporting such a view is far from conclusive and it is not very likely that these enormous quadrupedal marshdwellers could have been sustained by any food other than large amounts of green matter.

The Palaeopoda are represented by the Thecodontosauridae, the Plateosauridae, and the "Triassic carnosaurs." This last group has been demonstrated (Colbert, 1964; Charig *et al.*, 1965; Walker, 1964) not to have any relationships with the true, post-Triassic carnosaurs, and to be closely connected with (or even inseparable from, as maintained by Charig *et al.*, 1965) the first two families. The thecodontosaurids are medium-sized bipedal or semi-bipedal upland herbivores, known from different levels of the Upper Triassic of South Africa, China, Europe, and North America. The plateosaurids are large European and Asiatic (probably also South American) bipedal plant-feeders dwelling in lowlands. The carnivorous palaeopods are here considered as belonging to one distinct family, for which the name Gryponychidae must be used.[1] Though the facts of association of skull and postcranial bones are scarce and dubious, there is enough evidence to show that carnivorous palaeopods were living in the Upper Triassic. The convenience involved in placing these forms in families containing herbivorous dinosaurs is not very great, as one of the current criteria for family separation is distinction in ecological type. It is therefore preferable to separate the gryponychids as a carnivorous offshoot of the palaeopods, though recognizing that they are close to the other two families with which they share the same type of pelvis, tarsus, and limb structure.

All the palaeopods are closely related, and they are also very similar to the melanorosaurids and later sauropods, so that it makes sense to group both palaeopods and sauropods in a suborder Sauropodomorpha as proposed by Charig *et al.* (1965) and accepted by Romer (1966b). Charig *et al.* make a convincing case in claiming that this term, coined by von Huene (1932), is preferable to Pachypodosauria of the same author, a name applied to the unnatural assemblage of sauropods, "prosauropods," and carnosaurs. Within the Sauropodomorpha, the distinction of palaeopods and sauropods as infraorders is meaningful, as it adequately expresses the evolutionary situation. The sauropods seem to have played a secondary role during Triassic times, only evolving to full-fledged diversity and abundance after the close of that period. The palaeopods, most probably derived from a quadrupedal promelanorosaurid or melanorosaurid stock, represent the main radiation of Triassic Sauropodomorpha, and they evolved into both upland and lowland plant-eaters, and upland bipedal carnivores.

What do we know about the probable origin of the three groups of dinosaurs already well established at the very beginning of the Upper Triassic? Not too much, but at least enough to reveal that the history of the sauropodomorphs and coelurosaurs must be traced well back into the Triassic. Saurischian remains are known from the Middle Triassic of Argentina (Reig, 1963a) and Brazil (von Huene, 1942). The Argentinian fossils are rather abundant, and they come from the Ischigualasto beds, a formation that, following Romer (1966a) and Reig (1963a), contains a fossil assemblage that clearly belongs to the B type of faunas representing, perhaps, an upper Ladinian stage (i.e., the latest Middle Triassic). The Brazilian remains occur from the Santa Maria beds, which are generally agreed to be older than the Ischigualasto and roughly equivalent to the Manda beds of Tanganyika.

According to our present knowledge, the Argentinian material represents at least four genera of saurischians, only three of which have been described (Reig, 1963a). One genus is a very small, undescribed coelurosaur. Another coelurosaur is repre-

[1] Both Walker (1964) and Charig *et al.* (1965) have indicated that the name Palaeosauridae cannot be used, as *Palaeosaurus* Riley and Stutchbury is preoccupied by *Palaeosaurus* Geoffroy; Kuhn (1959) created the name *Palaeosauriscus* to replace the first name.

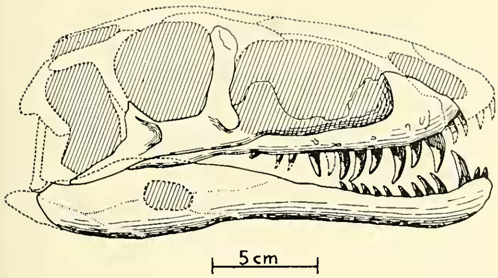

Figure 13. Lateral view of the skull of *Triassolestes romeri* Reig. (From Reig.)

sented by a podokesaurid, *Triassolestes* (Figs. 13, 14), known from skull and postcranial bones of two individuals.[1] The remaining two genera are obviously palaeopods. The best known is *Herrerasaurus*, a fairly large genus with specialized carnivorous dentition and typical palaeopod pelvis and posterior limbs (Figs. 14, 15), but with a peculiarly expanded distal border of the pubis, very like the situation in megalosauroid carnosaurs. As indicated by Walker (1964: 107), this last character-state does not necessarily imply a taxonomic or phylogenetic affinity between *Herrerasaurus* and the Upper Jurassic and Cretaceous true carnosaurs, and the genus must be placed in the Palaeopoda either as a member of the Gryponychidae or as a separate line. The other palaeopodan genus is *Ischisaurus*, known from incomplete remains of different individuals. It is thecodontosaurid-like in size and general appearance, and the small size of the humerus, which hardly exceeds half of the length of the femur, suggests that it was a definitely bipedal form.

A supposed Brazilian dinosaur has been described by von Huene as *Spondylosoma*, on the basis of isolated bones insufficient to allow of even ordinal assignment. Material recovered later, and being at present studied by Colbert, clearly indicates, however, that a saurischian of palaeopodian

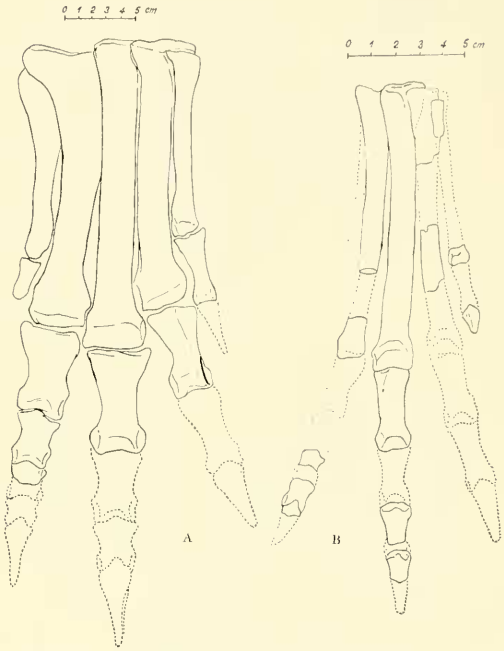

Figure 14. Pes in Middle Triassic saurischians from Ischigualasto, Argentina: A, *Herrerasaurus ischigualastensis* Reig; B, *Triassolestes romeri* Reig. (From Reig.) [See Addendum for systematic position of *Triassolestes*.]

affinities was present in the Santa Maria fauna.

The Sauropodomorpha and the Theropoda were thus well differentiated in the Middle Triassic (Fig. 16). It has been suggested (Charig *et al.*, 1965: 215–216) that these two major divisions of the Saurischia originated independently within the Pseudosuchia of the Middle Triassic.

I believe that there are good reasons to doubt that the sauropodomorphs could have arisen from Middle Triassic pseudosuchians, and I am more inclined to look for their ancestry in the Lower Triassic thecodonts. One important argument for this is the timing, as the origin of the sauropodomorphs must necessarily be placed at least as early as the very beginning of the Middle Triassic. This is the only way to explain that in the upper Middle Triassic they have already split into at least three different families: melanoro-

[1] See, however, the Addendum.

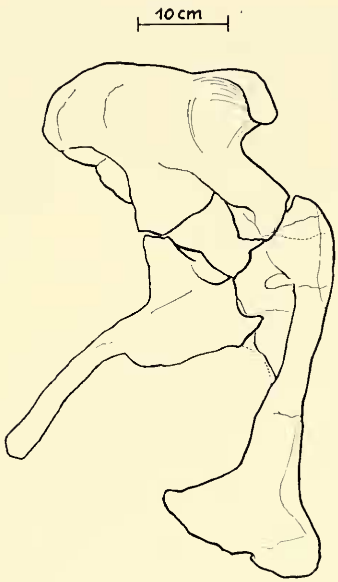

Figure 15. Pelvis of *Herrerasaurus ischigualastensis* Reig. (From Reig.)

saurids, gryponychids, and thecodontosaurids (Fig. 16). The other important argument is ankle morphology. As Krebs (1963) pointed out, the mesotarsal type of ankle joint of the saurischians is hardly derivable from the crocodiloid ankle of the Pseudosuchia. Therefore, the only groups to be considered in sauropodomorph ancestry, as required by ankle morphology, are the euparkeriids and the erythrosuchids, both of which combine the possession of a reduced carpal set with the lack of crocodiloid specializations. In the case of the euparkeriids, Ewer (1965: 431) pointed out that the ankle of *Euparkeria,* in spite of not being specialized as in later pseudosuchians, is advanced a bit towards a pseudo-mesotarsal articulation, which involves eventual elimination of the calcaneum, a situation that could have been ancestral to the "prosauropods" and sauropods. *Euparkeria* is, moreover, slightly built, potentially bipedal, and has dermal armor, all features not to be expected in the ancestor of the originally quadrupedal, morphs. It is more likely that the ancestry of the latter would be within the erythrosuchids, both on ecological and morphological considerations. In fact, it is not difficult to think of the huge, marsh-dwelling, quadrupedal erythrosuchids, with mesotarsal ankle and devoid of any armor, as the ancestors of the quadrupedal, large-sized, unarmored, and marsh-dwelling melanorosaurids (Fig. 16). At the same time, the euparkeriids are likely to be the ancestors of the coelurosaurians, since the evidence indicates that the latter have from the very beginning been upland, rapidly-moving bipedal carnivores, possessing a type of ankle joint which, in spite of being of mesotarsal type, has a calcaneum with a tuber, a condition reminiscent of the crocodiloid pseudosuchian tendencies. At the same time, the fact that at least one coelurosaurian (*Ceratosaurus*) has dermal armor can also be taken as an indication of an early pseudosuchian ancestry.

But, as a matter of fact, it is necessary to realize that we are at the very beginning of an explanation of saurischian origin. The views here advanced on the probable origin of sauropodomorphs from erythosuchid proterosuchians are only to be considered as working hypotheses that, in our belief, match the known facts better than do alternative interpretations. We must admit that these facts are so far not sufficiently complete to warrant a thorough reconstruction of early saurischian history. They are, however, at least complete enough to make it necessary to discard such generally accepted views as that the common origin of all the saurischians lay in bipedal, Upper Triassic pseudosuchians. It is also evident now that the radiation of the saurischians did not start after the extinction of the thecodonts. During Middle and Upper Triassic times, both taxa had their own extensive radiations, apparently developing not only parallel and competitive similar forms, but also forms differing in ecological roles and habitat preferences. The herbivores are by far the less common of the

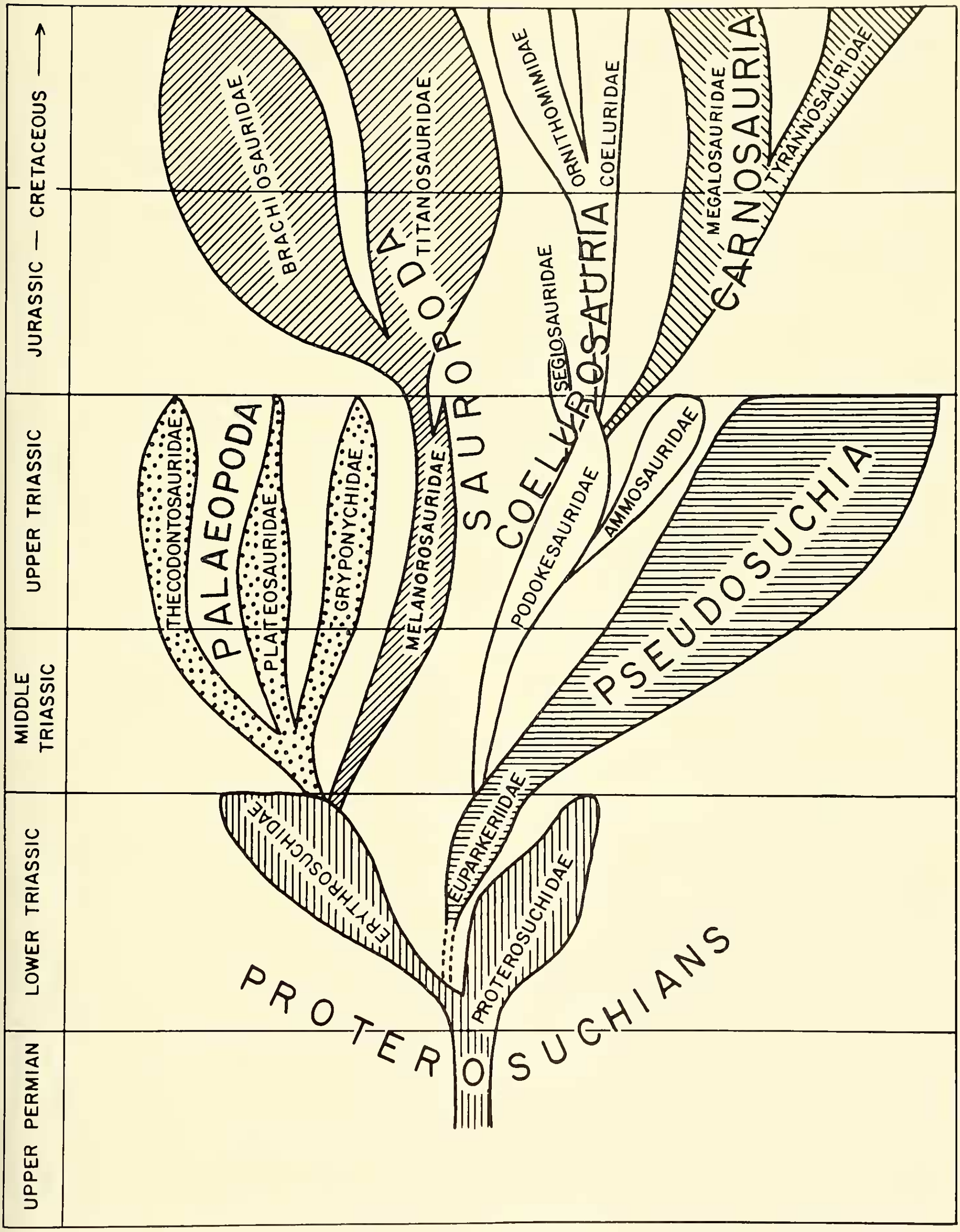

Figure 16. Phylogenetic diagram showing the suggested origins and the relationships of the major saurischian groups.

heavy-built, and unarmored sauropodo-Middle and Upper Triassic pseudosuchians and saurischians, being limited in fact to the stagonolepidids and the melanorosaurids. At these times gomphodonts and kannemeyeroid dicynodonts seem to have been competitors of plant-eating archosaurs.

The case of the phytosaurs and other archosaurian groups

In our present state of knowledge, the relevant evidence for advancing a serious hypothesis of the origin of the Pterodactyla and the Ornithischia is not available. The Pterodactyla, when first encountered in the Lower Jurassic, had already acquired the whole set of specializations for air locomotion. They were probably derived from lightly-built, arboreal pseudosuchians, and the fact that *Scleromochlus* is a genus with these characteristics supports the view that it was connected with the group from which those archosaurs adapted to flying could have arisen. This is as much as can be said at the moment.

As far as the Ornithischia are concerned, this order of dinosaurs, dominant in the Cretaceous, is rather obscure in origin. It has been maintained that the order had its first radiation prior to the Upper Triassic, because of the characteristics of incomplete remains from the Cave Sandstone beds of South Africa, which have been referred to two different genera: *Geranosaurus* and *Heterodontosaurus* (see Crompton and Charig, 1962). The evidence is, however, too fragmentary to support any such conclusion. Walker (1961) suggested that the stagonolepidids might be close to the ancestry of the ornithischians, but in this case also the evidence warrants only highly tentative speculations. The question of ornithischian origins is better considered an open problem until more information becomes available. The lack of relevant data on Triassic ornithischians could also be interpreted as an indication that their origin took place at a rather late stage of archosaurian evolution.[1]

The case of phytosaur origins seems to be a little less obscure, since we are at least able to postulate a probable ancestral group: the proterosuchids. The phytosaurs are a typical Upper Triassic group, and their association with saurischians and metoposaurid labyrinthodonts is the characteristic feature of the C type of Triassic faunas. No certain phytosaur remains are known from the Middle Triassic, but the Lower Triassic of Europe has afforded one skull, which is the basis of the genus *Mesorhinosuchus,* currently referred to this group. Recent work by Gregory (1962) casts some doubts upon the stratigraphic provenance and taxonomic position of this skull, and it must be admitted that the isolation of the specimen with respect to the whole remaining phytosaur record, together with the date and conditions of its discovery, justify a skeptical attitude. The probable presence of a phytosaur in the European Bunter, however, is to be admitted if we assume that the proterosuchians are the most likely ancestors of this group. And this is likely to be the case, since the phytosaurs, aquatic and primitive in postcranial morphology, are hardly derivable from the pseudosuchians, a group that from the outset shows specializations in the appendicular skeleton for a terrestrial way of life that clearly went beyond the level attained by similar advances in the phytosaurs. Admittedly, the phytosaurs share with the pseudosuchians several improvements in general organization, such as the presence of an otic notch, pterygoids joined at the midline, absence of palatal teeth, large antorbital fenestra, absence of intercentra, propodials largely moving in a vertical plane, and well-developed osteoderms. All these features can be interpreted as acquisitions connected with a better

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[1] Casamiquela (1967), however, recently described ornithischian remains from the Ischigualasto (upper Middle Triassic) beds. See Addendum.

adaptation both for locomotion on land and for predation that may well have arisen independently in different groups evolving from a proterosuchian condition. Besides these character-states, the phytosaurs show several specializations connected with improvements for aquatic life and aquatic predation: a very long and narrow rostrum formed largely by premaxillaries; external narial openings placed far behind the tip of the snout, close to the midline, between or at a short distance in front of the antorbital fenestra; orbits situated high in the skull; choanae placed posteriorly, and palatines forming lateral shelves below them, etc. The phytosaurs are to be considered specialized proterosuchid derivatives that evolved as amphibious predators, able to live a more efficient aquatic life than their forebears, and at the same time able to move about on the firm land around the water. They were probably very close to the modern crocodiles in biological type.[1]

SUMMARY OF THE MAJOR EVENTS IN EARLY ARCHOSAURIAN EVOLUTION

Improved knowledge of the organization of the first archosaurs, the proterosuchian thecodonts, and a re-examination of present evidence and interpretations of the phylogeny and taxonomy of the main archosaurian groups support the following reconstruction of the early events in the evolution of archosaurs:

1) The archosaurs arose during early Upper Permian times, probably from a branch of aquatic pelycosaurs, the Varanopsidae, which separated from the main line of pelycosaur evolution early in the Lower Permian.

2) During the uppermost Permian and the early Lower Triassic, the first recorded group of archosaurs, the proterosuchid proterosuchians, developed. These were primitive, aquatic predators, living mostly in permanent waters (lakes, ponds, and rivers), as important members of fresh-water communities. They survived until the upper part of the Lower Triassic, but dwindled in number and diversity.

3) Some populations of proterosuchids became better adapted to living in shallow waters and improved as predators of large animals. The erythrosuchid proterosuchians arose from such populations, and became dominant in swamps during the upper Lower Triassic.

4) The Pseudosuchia are first represented by the Euparkeriidae of the upper Lower Triassic. These were mostly quadrupedal, rather tiny, upland predators. Their origin is to be sought in the transitional phase of the proterosuchid-erythrosuchid descent.

5) In the uppermost Lower Triassic, the euparkeriids evolved into the rauisuchids. These were the large, quadrupedal, upland predators of the Middle Triassic.

6) The stagonolepidids arose from the euparkeriids in the Middle Triassic, becoming an important group in the Upper Triassic. They were upland dwellers, either scavengers or omnivores.

7) The euparkeriids probably survived through the Middle Triassic, and their last populations gradually were transformed into the ornithosuchids, which became a rather important group in the Upper Triassic as bipedal, medium-sized and large predators.

8) Perhaps on the borderline between Middle and Lower Triassic, the coelurosaurian saurischians evolved from a pseudosuchian, euparkeriid-like source. They were from the beginning bipedal, lightly-built, rapid predators inhabiting the upland environments. They were well established by the upper Middle Triassic, and became diversified and rather abundant in the Upper Triassic.

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[1] Walker (1968) has recently advocated that *Proterochampsa* is a phytosaur ancestor (see Addendum).

9) The true carnosaurs evolved in the uppermost Triassic or lowermost Jurassic from a coelurosaurian ancestor.

10) The sauropodomorph saurischians arose as true sauropods in the uppermost Lower Triassic, probably from erythrosuchid proterosuchians, and were four-legged, marsh-dwelling forms from the beginning. These first sauropods were a rather unimportant group in Middle and Upper Triassic times, represented only by the melanorosaurids in the known record.

11) The first important radiation of the sauropodomorphs developed within the framework of the infraorder Palaeopoda. Palaeopod saurischians probably evolved from the first sauropods and radiated in Middle and Upper Triassic times into herbivorous and carnivorous lowland and upland forms. They included partially bipedal and completely bipedal forms.

12) The first crocodiles were the Middle Triassic Archaeosuchia. They probably arose from the last proterosuchid populations of the uppermost Lower Triassic, within the framework of the freshwater communities, but evolved adaptations for a more amphibious way of life. They seem not to have been an important group in the freshwater environments of the Upper Triassic, perhaps because of the competition of the phytosaurs, dominant at this time.

13) During the Upper Triassic, an offshoot of the archaeosuchians became better adapted for terrestrial life and spread as a group of upland predators: the protosuchian crocodiles.

14) The phytosaurs probably evolved from the proterosuchids in the late Lower Triassic as members of the freshwater communities. They were unimportant in the Middle Triassic, perhaps because of the competition of the Archaeosuchia, and became dominant freshwater predators only in the Upper Triassic.

15) By the end of the Triassic, several groups of archosaurs had become extinct: pseudosuchians and protosuchians, and probably archaeosuchians, phytosaurs, and palaeopod saurischians. It was the beginning of the second phase of archosaurian evolution, a phase in which sauropods, carnosaurs, coelurosaurs, mesosuchian crocodiles, pterosaurs, and, later, ornithischians, deployed as full-fledged archosaurian groups.

EVOLUTIONARY AND TAXONOMIC CONCLUSIONS

The foregoing statement of the major events of the early phase of archosaurian evolution and the previous discussion of the evidence supporting such conclusions, are full of implications for the theoretical problems posed on pages 230ff. and 245ff. of this paper.

It will be of interest, now, to examine to what extent the described patterns of origin both of the archosaurs as a major group and of the groups within the archosaurs agree with the current concepts about the processes involved in the emergence of new major taxa. I have already said that a shift into a new adaptive zone, a speeding up of the evolutionary change in the transitional region between the original and the new adaptive zone, and the sudden appearance of key innovations opening new evolutionary possibilities are alleged to occur in the origin of new supraspecific taxa. This process would be responsible for the creation of apparent discontinuities that afford a clear-cut borderline between the original and the descendent groups. We have also seen that Bock (1965) claimed that this alleged pattern is an oversimplification; he emphasized the step-wise character of the process leading to the emergence of a new taxon, a process that he thought of as involving a more complex pattern than any single-phase change from one adaptive zone into another.

Let us examine, first of all, to what extent the shift into a new adaptive zone is exemplified by archosaur origins and the origin of the subordinate major taxa of archosaurs.

In fact, the origin of the archosaurs as a whole does not seem to be associated with a major shift between two different adaptive zones. The probable archosaur ancestors were water-adapted pelycosaurs, and the first known archosaurs were water-dwelling animals. Both ancestors and descendants seem to have been predaceous animals. Although it must be admitted that a considerable gap exists between the proposed ancestral group and the derived one, the process of the emergence of the archosaurs is likely to have been one of gradual improvement toward a more efficient life in the same general adaptive zone.

As far as the origins of the various archosaurian subordinate taxa are concerned, the pattern seems to have been a mixed one. There is an actual shift from lowland, marsh habitats toward upland environments in the passage from the proterosuchians to the pseudosuchians, but the passage from the proterosuchians to the crocodilians, phytosaurs, and sauropods does not seem to have involved any major departure from the general environments inhabited by the ancestral forms. The same is the case if the coelurosaurians were derived from the euparkeriid-like pseudosuchians. But a shift did occur from the archaeosuchians to the protosuchians. These various cases indicate that a major shift between two distinct general adaptive zones is not necessarily connected with the emergence of a major taxon, though it may occur in certain cases.

If we take a large scale approach, we could, however, agree that there is a major shift in general adaptive zone between the time of the appearance of the archosaurs and the time of their achievement of dominance at the beginning of the Jurassic. The first archosaurs were strictly water-tied animals, swimming and feeding in lakes, ponds, and rivers; the post-Triassic ones were enormous swamp-dwellers and upland forms. The intermediate zone is, however, a long-lasting one, in which various minor radiations took place, and in which there is no reason to postulate any special acceleration of the evolutionary changes.

The hypothesis of an evolutionary speeding up in an alleged transitional zone is also not supported by the known cases of an actual shift. As already stated, the origin of the Pseudosuchia can be considered as one of the cases in which an actual switch seems to have occurred. Nevertheless, we can see here that the process was a gradual and long-term one, and that even the first definite pseudosuchians, the euparkeriids, were transitional in several respects.

Key innovations have arisen, as we have seen, several times in the early evolution of archosaurs. Character-states such as the development of an antorbital fenestra, the acquisition of an otic notch, the shifting forward of the mandibular articulation, the upright stance of the propodials, the pseudosuchian-crocodiloid ankle joint, to mention only some examples, can be safely regarded as being connected with improvements in general adaptability, thereby opening new evolutionary possibilities. It is interesting to realize, however, that features such as the above probably arose independently in different groups, and even that some of them, like the antorbital fenestra, had already evolved at a pre-archosaurian level of evolution.

The general pattern of the emergence of major taxa, as exemplified by the case of the archosaurs, seems to be a pattern of gradual and long-lasting change. At least seven different processes are involved: (1) steady development of the typical characters of the emerging taxon; (2) exploratory radiations into new adaptive zones; (3) competition between lineages that achieve a similar ecological role from different ancestries; (4) steady acquisition of key characters opening new evolutionary possibilities in different lineages;

(5) improvement within the framework of a generally similar adaptive zone; (6) gradual shift into new adaptive zones; and (7) gradual replacement of successive groups until eventually a new, major taxon becomes established. No factors different from those involved at the species or infraspecies level need be involved. Although it may be convenient, for the sake of the description of the evolutionary events, to distinguish the different processes of evolution [as did Huxley (1958) and other authors], it must be stressed that the final agencies of evolutionary change are really the same for any of the processes distinguished in the description of large-scale evolutionary phenomena.

Thus, the emergence of a new taxon can be considered a phenomenon plainly involving only evolution governed by selection and by the known processes of change in gene frequency within populations; the regular processes of evolution at the species level therefore, are also those responsible for the gradual, progressive establishment of major taxonomic groups. On the other hand, the latter are to be considered not as artifacts of classification but as natural units, for they include subordinate entities connected by relationships of origin and descent. But they are not bounded by discontinuities, these being only imposed by the incompleteness of the record. The fact is that the better the evidence connected with the origins of a major group is known, the less apparent are the alleged discontinuities between the ancestral and the descendent groups.

The concepts having natural taxa as referents are hence necessarily polythetic concepts, and a fringe of vaguenesss seems to be unavoidable in the statement of the intension of taxonomic concepts at the supraspecific level. It also seems necessary to agree that vagueness can occur in the statement of the extension of these concepts, as intermediate forms can always be placed in either of the groups they connect.

RESUMEN

Nuevos conocimientos sobre la organización de los tecodontes proterosuquios, que son los más antiguos y los más primitivos reptiles conocidos de la subclase Archosauria, conjuntamente con un estudio crítico de los datos y las interpretaciones actuales sobre la filogenia y la clasificación de los principales grupos de reptiles arcosaurios, dan fundamento a la siguiente reconstrucción de los acontecimientos que tuvieron lugar durante el comienzo de la evolución de los arcosaurios:

1) Los arcosaurios surgieron durante el comienzo del Pérmico superior a partir, probablemente, de una rama de pelicosaurios acuáticos, los Varanopsidae, que se separaron de la línea principal de la evolución de los pelicosaurios en el Pérmico inferior.

2) Durante el Pérmico más superior y el comienzo del Triásico inferior se desarrolló el primer grupo conocido de reptiles arcosaurios, los tecodontes proterosuquios de la familia Proterosuchidae. Los proterosúquidos fueron predadores acuáticos primitivos que vivían en aguas dulces permanentes (lagos, pantanos y ríos) constituyendo una parte importante de las comunidades dulceacuícolas de la época. Sobrevivieron hasta la parte superior del Triásico inferior, aunque en menor número y más reducidos en diversidad.

3) Algunas poblaciones de proterosúquidos se hicieron mejor adaptados para vivir in aguas someras y se perfeccionaron como predadores de grandes herbívoros semiacuáticos. Los proterosuquios de la familia Erythrosuchidae surgieron de dichas poblaciones, tornándose dominantes en los pantanos de la parte superior del Triásico inferior.

4) Los primeros representantes del suborden Pseudosuchia de tecodontes fueron los euparkéridos de la parte superior del Triásico inferior. Eran predadores terrestres de tamaño pequeño y de locomoción

cuadrúpeda. Su origen debe buscarse en la fase transicional de la transformación de los proterosúquidos en eritrosúquidos.

5) A finales del Triásico inferior, los euparkéridos dieron lugar a los rauisúquidos. Estos fueron predadores terrestres de gran tamaño y de andares cuadrúpedos que prosperaron principalmente en el Triásico medio, donde están representados por géneros como *Prestosuchus, Saurosuchus* y *Stagonosuchus.*

6) Los Stagonolepídidos (familia que incluye a aetosáuridos y stagonolépidos) surgieron probablemente de los euparkéridos en el Triásico medio, tornándose un grupo importante de las faunas terrestres del Triásico superior. Fueron reptiles terrestres acorazados, de hábitos alimentarios omnívoros, o carroñeros.

7) Es probable que los euparkéridos sobrevivieron durante el Triásico medio, época en la que se fueron transformando gradualmente en los ornitosúquidos. Estos constituyen un grupo de predadores bípedos de tamaño mediano y grande de importancia en las comunidades terrestres del Triásico superior.

8) Es posible que los dinosaurios saurísquios del grupo de los celurosaurios hayan surgido de una cepa pseudosuquia afín a los euparkéridos en la transición entre el Triásico inferior y el Triásico medio. Los celurosaurios fueron desde su origen predadores terrestres bípedos y esbeltos. Estaban ya bien representados en la parte final del Triásico medio, pero se hicieron más abundantes y diversificados en el Triásico superior, donde competían con los ornitosúquidos.

9) Los verdaderos dinosaurios carnosaurios evolucionaron en el Triásico más superior o en el Jurásico más inferior, a partir de un ancestro celurosaurio.

10) Los dinosaurios saurísquios del grupo de los Sauropodomorpha, surgieron como verdaderos saurópodos a finales del Triásico inferior, probablemente a partir de los proterosuquios de la familia Erythrosuchidae. Desde el comienzo fueron animales cuadrúpedos habitantes de los pantanos. Estos primeros saurópodos constituyen un grupo relativamente poco importante en el Triásico medio y en el Triásico superior, donde están representados solamente por los melanorosáuridos.

11) La primera radiación importante de los sauropodomorfos se desarrolló en el marco del infraorden Palaeopoda. Los saurisquios paleópodos surgieron probablemente de los primeros saurópodos y radiaron en el Triásico medio y superior en varias formas herbívoras y carnívoras que vivían tanto en los pantanos como en las tierras altas, entre los que se encontraban animales parcialmente bípedos y otros totalmente bípedos.

12) Los primeros cocodrilos fueron los Archaeosuchia del Triásico medio. Es probable que los arqueosuquios surgieran de las últimas poblaciones de proterosúquidos en la parte más superior del Triásico inferior, en el contexto de la comunidad dulceacuícola, pero desarrollando adaptaciones para una vida más anfibia. No parecen haber sido un grupo importante en los ambientes de agua dulce del Triásico superior, quizás por la competencia de los fitosaurios.

13) Durante el Triásico superior, una rama de los arqueosuquios se tornó mejor adaptada para la vida terrestre y se desarrolló como un grupo de predadores no acuáticos convergente con los pseudosuquios y los celurosaurios: los cocodrilos protosuquios.

14) Los fitosaurios probablemente se originaron en los proterosúquidos a finales del Triásico inferior, en el seno de las comunidades dulceacuícolas. Fueron poco importantes en el Triásico medio, posiblemente por la competencia con los arqueosuquios, pero se hicieron predadores dulceacuícolas dominantes durante el Triásico superior.

15) A finales del Triásico, se extinguieron varios grupos de arcosaurios: pseudosuquios, protosuquios, probablemente también los arqueosuquios, los fitosaurios y los saurisquios paleópodos. Estas extinciones marcan el comienzo de la segunda fase de la evolución de los arcosaurios, caracterizada por la expansión de los saurópodos, los carnosaurios, los cocodrilos mesosuquios, los pterosaurios y los ornitisquios.

Los enunciados anteriores sobre los acontecimientos probablemente suscitados en la fase temprana de la evolución de los arcosaurios tienen variadas implicaciones de interés en la cuestión de la clasificación y el origen de los grupos taxonómicos de rango superior.

El problema del origen de los arcosaurios y de los grupos subordinados de arcosaurios se relaciona con la cuestión ampliamente debatida del origen de los taxa de rango superior. La tesis más difundida para explicar el origen de los taxa de rango superior sostiene que en el proceso de evolución de tales taxa, se produce la invasión de una nueva zona adaptativa, la aceleración del ritmo evolutivo en la zona transicional entre la zona adaptativa original y la nuevamente conquistada, y el surgimiento súbito de innovaciones evolutivas que abren nuevas posibilidades de expansión en la nueva zona. A través de estos procesos, se originaría una clara discontinuidad entre el taxón original y el taxón descendiente, que haría relativamente fácil la distinción entre los mismos. Bock (1965) sostuvo que esa tesis implica una simplificación excesiva de la marcha real de los acontecimientos, y destacó el caracter gradual del proceso de la emergencia de un nuevo taxón, proceso que involucraría fenómenos más complejos que un cambio producido meramente al pasar de una zona adaptativa a otra.

La descripción que hemos hecho en lo que antecede de los principales acontecimientos vinculados con el origen y la primera diferenciación de los arcosaurios, confirma las objeciones señaladas por Bock. El origen de los arcosaurios como tales no parece estar asociado con un cambio adaptativo importante. Tanto los antecesores de los arcosaurios como los primeros arcosaurios (los proterosúquidos) eran animales acuáticos y carnívoros. Es muy probable que el origen de los proterosúquidos sólo haya involucrado un perfeccionamiento gradual hacia una vida más eficiente en la misma zona adaptativa general. El analisis del origen de los grupos subordinados de arcosaurios, indica que tampoco se puede postular un cambio brusco hacia distintas zonas adaptativas como fenómeno inseparable del surgimiento de nuevos grupos. Sin embargo, si observamos el proceso en su perspectiva general, podemos coincidir en la existencia de un cambio en la explotación de distintas zonas adaptativas desde la época de la primera aparición de los arcosaurios hasta la época de la culminación de su dominancia al comienzo del Jurásico. Los primeros arcosaurios eran creaturas estrictamente acuáticas y carnívoras, mientras que las formas jurásicas eran enormes herbívoros terrestres o anfibios y diversos tipos de carnívoros terrestres. La transición entre estos dos extremos, sin embargo, ocupó la mayor parte del Triásico, y durante ese período tuvieron lugar diversas radiaciones exploratorias en el marco de la competencia por la explotación de distintos recursos alimentarios. No queda lugar, entonces, para suponer un proceso en una solo fase ni una aceleración especial de los ritmos evolutivos.

El proceso general de la emergencia de un taxón de rango superior, como surge del ejemplo de los arcosaurios, parece más acorde con la idea de un proceso de cambio gradual y de larga duración, que involucra sencillamente el juego de las fuerzas evolutivas conocidas para la evolución al nivel de la especie: cambios en la frecuencia génica en las poblaciones y selección natural.

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ADDENDUM

After this paper was submitted for publication, some important contributions appeared that are relevant to several of the topics herein discussed.

The question of crocodile origins and the evolutionary meaning of *Proterochampsa* merited a paper by Walker (1968) that introduced radical changes in previous interpretations, including the views sustained in this paper. Walker affords a new look at the cranial structure of *Stegomosuchus* on the basis of casts procured by Dr. Romer, which allowed him to reinterpret the roof of the skull of *Protosuchus* as known from the photographs given by Colbert and Mook (1951). On the basis of these new interpretations, and of similarities in the dermal scutes, Walker concluded that *Stegomosuchus* is closely related to *Protosuchus,* and even that *Stegomosuchus longipes* could be a juvenile of *Protosuchus richardsoni.* Furthermore, in his view, the skull of *Protosuchus* indicates that this genus is much more closely related to *Notochamsa* than was previously maintained. Thus, his conclusion is that these three genera are to be placed in a single family of the suborder Protosuchia of crocodiles, a family that, by priority, should be named Stegomosuchidae.

Although I accept that some of these views might be proved as well substantiated by further work on the actual specimens of these forms, I hardly think it justified to propose such drastic changes without observing the original specimens. The same criticism applies to Walker's reappraisal of the phylogenetic place of *Proterochampsa.*

Walker analyzed 16 characters, most of which would afford "ample evidence for regarding *Proterochampsa* as a very primitive phytosaur, and not a crocodile" (1968:

11). This conclusion is, of course, of great interest, but here again the foundations might be suspected, due to the lack of direct observations of the several available specimens of the discussed genus. Moreover, Walker bases a part of his argument on my first description of *Proterochampsa* (Reig, 1959), a description which has been corrected by Sill's work (1967), based on broader comparisons and on more specimens, some of them better preserved.

There is not the space here to attempt a thorough discussion of Walker's arguments on the place of *Proterochampsa*. I wish to advance, however, my feeling that several parts of his analysis deserve serious consideration and a careful checking in the light of the actual specimens. Nevertheless, I am strongly convinced that, until this work is accomplished, it is wiser to maintain Sill's interpretation of *Proterochampsa* as the correct one, as, furthermore, it is the only one which is based on direct comparisons.

Another interesting suggestion in Walker's paper is his belief that *Cerritosaurus* (here considered as a probable junior synonym of *Rhadinosuchus*) possesses "some at least of the attributes one expects to find in a crocodile ancestor" (Walker, 1968: 11–12). We have already mentioned the isolated position of this genus among the Pseudosuchia, and the difficulties that arise in tracing its origins from the early and central Pseudosuchian family Euparkeriidae. Thus, Walker's suggestion seems to deserve serious consideration here, as it is likely to make more balanced the phylogenetic scheme of the Pseudosuchia.

Needless to say, new evidence might also be critical for the testing of Walker's views, and this evidence may already be available through Romer's and Bonaparte's new findings in the pre-Ischigualasto Chañares formation of La Rioja (Romer, 1966a, and *in press*). These two colleagues found excellent specimens of a small archosaurian showing significant resemblances to *Proterochampsa* (Romer and Bonaparte, pers. comm.). The animal, still undescribed, could be the key to the correct interpretation of *Proterochampsa* and other early crocodiloid forms, including the awkward "*Cerritosaurus*."

Furthermore, new light on the question of early crocodilian history will surely be shed by Bonaparte's recent findings in the Upper Triassic Los Colorados Beds of Ischigualasto (Bonaparte, 1969, in press.). These findings, still mostly undescribed, include two crocodiloid archosaurians. One of them is closely related to *Sphenosuchus* and *Hesperosuchus*, the other resembles *Protosuchus*. The former is also related to *Triassolestes romeri* from the Ischigualasto beds, an archosaur which I described (Reig, 1963) as a saurischian dinosaur. In that paper, I tentatively referred to *Proterochampsa* a fore-limb showing the typical carpal structure of crocodiles associated with the type skull of *Triassolestes romeri*. Now, the *Sphenosuchus*-like new archosaurian from Los Colorados found by Bonaparte (Pers. comm. and 1969), which include both cranial and postcranial material, allowed him to conclude that the fore-limb associated with *Triassolestes*' skull actually belongs to the same individual represented by the skull. *Triassolestes* is to be interpreted, therefore, as a primitive crocodilian of the group of "dinosaur-like crocodiles."

In all likelihood, after these new findings of the Argentinian Middle and Upper Triassic are described, we shall have a better understanding of the various crocodiloid forms currently classified as Protosuchids, Notochampsids, Sphenosuchids, etc. We can suppose, therefore, that a new appraisal of early crocodilian history will come in the near future.

A recent description of ornithischian dinosaur remains from the Ischigualasto beds (Casamiquela, 1967) makes it necessary to change some of the tentative conclusions of previous pages on the time of origin of this taxon. Although the new findings, described as *Pisanosaurus mertii*, are too fragmentary to afford precise observations on the problem of Ornithischian ancestry, they are conclusive first of all in proving the presence of a full-fledged ornithopod in the upper Middle Triassic of Argentina, and secondly, in tracing the origin of ornithischian dinosaurs well into the early Middle Triassic, that is to say, at the very beginning of the first diversification of the non-proterosuchian archosaurs.